# ZOOLOGICA

SCIENTIFIC CONTRIBUTIONS

*of the*

NEW YORK ZOOLOGICAL SOCIETY

VOLUME 35

1950

Numbers 1-20

Published by the Society

The Zoological Park, New York

# CONTENTS

## Part 1. April 17, 1950.



## Part 2. August 1, 1950.



## Part 3. November 27, 1950



## Part 4. December 30, 1950.

# ZOOLOGICA

SCIENTIFIC CONTRIBUTIONS

*of the*

NEW YORK ZOOLOGICAL SOCIETY

VOLUME 35

Part 1

Numbers 1-5



Published by the Society

The Zoological Park, New York

April 17, 1950

# CONTENTS

# 1.

## Proceedings of the Second Conference on the Biology of Normal and Atypical Pigment Cell Growth.

### Foreword.

The second conference on the Biology of Normal and Atypical Pigment Cell Growth was called in direct response to the requests of a group of biologists, biochemists, biophysicists and medical research workers who wanted another opportunity for an exchange of ideas between specialists in different fields. They wanted to learn firsthand the results of recent experiments and observations.

The second conference was held at the New York Zoological Park on November 18-19, 1949.

The publication of "The Biology of Melanomas" by the New York Academy of Sciences, which sponsored the first conference in 1946, established Pigment Cell Growth as a united topic and brought its subject matter into focus and prominence. The many new contributors to the second conference testify to the growth of interest in the nature and behavior of the pigment cells. Among these contributors are some whose researches in the field go back a quarter of a century. The pool of information has been greatly enriched and the present publication will make it accessible to an ever-widening group of investigators.

The abstracts published here differ somewhat from those originally submitted for distribution prior to the conference. They have been expanded and contain references to the most recent papers dealing with pigment cell growth and related topics. This report also includes discussions and the introductory remarks made by the chairmen of the four sessions of the conference.

The next conference will be organized in response to the future needs of investigators in the broad field of pigment cell growth. Suggestions and inquiries will be welcomed at all times by the organizing chairman.

### Acknowledgments.

The conference is indebted to Dr. George M. Smith of the Yale University School of Medicine for his continuing interest in these meetings. As Medical Advisor to the Anna Fuller Fund, he recommended that a grant be made to the New York Zoological Society to defray part of the costs of arranging and conducting the conference. In this connection, the organizing chairman wishes to acknowledge the many valuable suggestions made by Dr. Smith that were put in action before and during the meeting. The thanks of the conference are also due to the New York Zoological Society for a grant in aid of publication of these abstracts.—Myron Gordon, *Genetics Laboratory of the New York Zoological Society, the American Museum of Natural History, New York* 24, *N. Y.*

## Abstracts.

### Table of Contents.

## *First Session: Clinical and Pathological.*

### Introduction.

Harry S. N. Greene.
*Yale University School of Medicine, New Haven, Conn.*

With increasing knowledge of the natural histories of tumors, it has become more and more apparent that there are many neoplastic diseases rather than one. Conferences for the separate consideration of specific tumor types are now the fashion and in no instance is this more fully justified than in the case of the melanomas. The well marked peculiarities of such tumors, with their failure to conform to the more or less conventional lines of behavior established by the more orthodox carcinomas and sarcomas, set them apart as black sheep of the neoplastic family and engender the necessity for individual study and special examination.

The source of the neoplastic cell, its development to biological autonomy and mode of dissemination, constitute problems differing in their fundamental conditions from those associated with other tumors. Fortunately, the differing conditions tend to facilitate investigation and, by their anomolous nature, may suggest fertile approaches to the general cancer problem. The occurrence of melanoblasts in heterotopic aggregates called nevi, presents an unparalleled situation in neoplastic disease, for here, assembled by some dysontogenetic process in convenient, lasting foci, are the cells intrinsic to the disease. By virtue of location in readily accessible, non-vital regions, the conversion to neoplastic elements and the development of the properties of invasibility and metastasizability are open to morphological and biological investigation as well as to clinical study. Further, the indiscriminate incidence of nevi with occurence in different locations, sexes and races, and their persistence throughout the different age periods and endocrine disturbances of an individual's life, allow an assessment of the significance of constitutional, intrinsic factors in the biological progress of the lesion.

One of the more marked variations from the behavior pattern of other tumors concerns the dissemination of the melanomas. The mode of spread in general neoplastic disease is by lymphatic extension or metastasis and it is customary to explain the occurrence of secondary foci of melanomas as a result of one of these processes. There is no question that fully developed, autonomous melanomas follow such routes of spread, but there is both clinical and experimental evidence to suggest that secondary foci may occur before the primary tumor attains the ability to metastasize. For example, when a secondary focus is found as far distant from a primary tumor in the scalp as a popliteal node, it is generally considered to be a blood-borne metastasis. Yet, if such a node is removed, the patient may survive for a number of years with no further evidence of tumor spread. Inasmuch as blood-borne metastasis entails the entrance of tumor cells into the blood stream with eventual lodgement and growth in multiple foci, it would appear either that the popliteal node represented the rare phenomenon of solitary metastasis or that in actuality it was not a metastasis at all. Evidence favoring this latter possibility is obtained from transplantation experiments. It appears to be a rule that all tumors capable of metastasis (and therefore all metastases) are hetero-transplantable; yet, it has been a frequent experience that nodes of the type cited above fail to grow when transferred to guinea pigs. Successful transplantation portends death, the survival period after heterologous growth averaging six months. It must be concluded from this either that the rule of transplantability applicable to other tumors does not hold in the case of melanomas, or that a different mechanism of dissemination exists. The point should not be labored in the present context and is mentioned only to emphasize an unexplored possibility of potential significance to an understanding of the tumors to be discussed.

The problems presented by the behavior of the melanotic tumors pertain to many different disciplines. The embryologist, the biochemist, the geneticist, the endocrinologist, the clinician, and even the pathologist, recognize fields of interest, and a definite hazard exists that the fruits of such interest may be limited by scope or publication to the individual specialty. It would appear to be a primary purpose of this conference to counteract the biased inclination of special interests and to emphasize that while the melanoma provides an excellent tool for the biochemist to study biochemistry; the embryologist, embryology; the geneticist, genetics, etc., the central problem concerns the melanoma as a malignant tumor.

## Malignant Melanoma Associated with Pregnancy.

ISABEL M. SCHARNAGEL & GEORGE T. PACK.
*Memorial Hospital, New York.*

More than a thousand cases of malignant melanoma have been observed and treated in the Memorial Hospital and in other hospitals by the staff of the Pack Medical Group during the past thirty-two years (since 1917). The primary melanomas are located on all parts of the body integument, including the skin, palms of hands, soles of feet and nail beds. In addition, there are malignant melanomas involving the paranasal sinuses, oral mucosa, anus and rectum, meninges, and choroid of the eye.

We have been especially interested in studying the hormonal influences on pigmented tumors. The development of pigmented nevi at puberty is well known, and the peculiar benign nature of pre-pubertal or juvenile melanomas in young children, in spite of their malignant histological structure, has been made a subject of special study.

Pregnancy is another period of altered hormone balance when many temporary and permanent pigmentations of the skin develop. There is often growth of a pre-existing pigmented nevus, fortunately not always to a malignant melanoma, as we have proved by excising them for histologic study. In 28 of our patients with malignant melanoma, however, the melanoma has seemed to develop in a pre-existing nevus during pregnancy, or else a pregnancy has come in a patient with malignant melanoma and has hastened the growth. Eight of our 28 patients with malignant melanoma gave history of the growth of a pre-existing pigmented tumor during pregnancy. Ten others presented themselves for treatment during the pregnancy with the malignant melanoma present and in some stage of development.

We both remember very graphically a young 28-year-old woman who very early in the course of her disease presented a picture of a very advanced melanomatosis, showing multiple dark blue-black cutaneous nodules in the region of the right chest wall, shoulder, arm and back. This young woman was in the fifth month of her pregnancy when she noticed the small lesion on the back in the right scapular region, which became red and sore. She visited a local hospital about a month later, where it was removed by a small excision, leaving a scar 3 cm. long. About four weeks later it grew back in the scar and she called attention to it when reporting for prenatal care. It was again removed with a skin segment about twice as big as the first. When she reached the eighth month of gestation, the pregnancy was interrupted by bag induction. A normal five-pound baby was delivered spontaneously. About a month later, a radical right axillary dissection was done and the specimen showed extensive metastases in the lymph nodes. Four months later, and eight months after the original excision, the multiple skin nodules appeared and the skin of the face and chest had a bluish cast. There were numerous shiny blue-black nodules and marked melanuria. She did not yet have demonstrable visceral metastases, but a few months later the spleen was markedly enlarged and very hard. When she died, sixteen months after her admission to us and fourteen months after the delivery, postmortem examination showed the most extensive cutaneous, subcutaneous and visceral involvement that one can imagine. Black nodules studded absolutely all the tissues.

The end-result has been fatal in fourteen, or 50%, of these patients, in three years or less. Of the patients treated over five years ago, only three survived, and only two are known to live over a five-year period, as one was lost to observation after four years. Those two are living eight and thirteen years, respectively, and are considered cured. One patient has had two normal pregnancies and deliveries at a safe interval after the radical surgical removal of the malignant melanoma which had not metastasized to the regional lymph nodes when they were dissected out.

All the patients treated within fairly recent years have had radical surgical treatment, including not only the wide excision of the site of the primary melanoma, but dissection continuously to the regional lymph nodes and radical removal of the lymph-node-bearing area. A 35-year-old woman may be used to illustrate this method of treatment. She presented herself for treatment with a lesion on the back and giving the following history: For four years she noticed something on her back. Four months before, while she was pregnant, it began to ulcerate and have a discharge. She consulted her family physician, who removed it by electrodesiccation. It grew back within a month. The following month she delivered a normal child. When we saw her, she had a raised, firm, bluish to brown growth 10 by 15 mm. in the margin of a scar situated in the midline of the back between the scapulae. At that time she had two small lymph nodes palpable in one axilla and larger hard ones in the opposite one. The malignant melanoma on the back was excised with a skin segment 5 to 6 cm. wide above and below and extending continuously to the axilla on each side. The subcutaneous fat and fascia over the muscles were removed more widely across the back and to each axilla. The axillary veins were dissected free of all fat and lymphoid tissue up to a level behind the pectoralis minor muscle. The axillary tissue on either side was removed in continuity with the tissue from the back. The microscopical examination confirmed the clinical diagnosis of metastatic melanoma in the lymph nodes from both axillae. In spite of this very radical surgery, a year later this patient had palpable hard nodules in both breasts. Both breasts were removed completely and there were two masses representing metastatic

melanoma in the right one and five in the left breast. Metastatic nodules next made their appearance in the neck and then in the liver, and in less than two years after her delivery and treatment, she died of malignant disease.

We have eleven patients in this series living and well at the present time, but most of them have been operated upon within the past two years.

These original observations are clinical, but may be summarized as follows:

(1) The benign or premelanotic nevus is definitely stimulated by hormonal changes of puberty and pregnancy.

(2) Pre-pubertal melanomas possessing all the histologic features of malignant melanoma except blood and lymph vessel invasion do not metastasize until puberty (with rare exception).

(3) Certain benign nevi are prone to change to malignant melanoma during pregnancy.

(4) Malignant melanomas grow with great rapidity, metastasize early and widely, are more malignant and have a lower rate of curability during pregnancy.

(5) Dormant, silent, residual melanoma may flare into active recurrence during pregnancy, subsequent to operative removal.

(6) Prophylaxis is removal of all suspicious nevi in women before or at least early during pregnancy.

BIBLIOGRAPHY.

SCHARNAGEL, ISABEL M. Treatment of Malignant Melanoma of the Skin and Vulva at Radiumhemmet, Stockholm. *Acta Radiol.*, 14:473, 1933.

——— Melanoma of the Skin. *J.A.M.W.A.*, June, 1946.

SCHARNAGEL, ISABEL M., G. T. PACK and MASON MORFIT. Principle of Excision and Dissection in Continuity for Primary and Metastatic Melanoma of the Skin. *Surgery*, 17, 6:849-866, June, 1945.

PACK, GEORGE T. Subungual Melanoma. *Bull. Memorial Hospital*, 2:24-28, Feb., 1930.

——— A Clinical Study of Pigmented Nevi and Melanomas. In: The Biology of Melanomas, New York Academy of Sciences, IV, pp. 52-62, Jan., 1948.

Questions of HERMAN CHARACHE,
Brooklyn Cancer Institute, New York.

1. In your experience with over one thousand cases of malignant melanoma, did you find whether melanuria is of any prognostic value?

*Answer*: We believe that melanuria is very frequently present in cases of malignant melanoma. There are other conditions also in which this reaction may be demonstrated. We do not believe that it has any important prognostic value.

2. Is the color of pigmented nevi, such as black, brown or blue, of any prognostic significance?

*Answer*: It has long been our practice to excise all blue-black moles, no matter how benign they appear. Of course many of these moles are Jadassohn neuronevi. These nevi are considered not to undergo malignant degeneration very often, but we have cases in which it has occurred. Otherwise, there is no great significance in the color of the moles, as a certain percentage of malignant melanomas contain no pigmentation at all. These non-pigmented melanomas may, however, produce pigmented metastases in lymph nodes. The color, therefore, has no great prognostic significance.

3. Would you recommend sterilization of young women with malignant melanoma, or interrupt early pregnancy in women with malignant melanomas?

*Answer*: The sterilization of young women with malignant melanoma seems to us a rather drastic procedure, as we believe that with radical surgery in early stages, we are able to cure these patients. I have cited one case where a woman is living and well for thirteen years and has had two normal pregnancies with deliveries since her malignant melanoma was treated, although it developed during the course of her first pregnancy. This woman had a spontaneous interruption of the first pregnancy, and I personally believe that if the malignant melanoma is diagnosed early enough in pregnancy so that therapeutic abortion can be carried out safely, it should be done.

## Benign and Malignant Neoplasia of Melanoblasts Through the Eyes of the Dermatologist.

S. WILLIAM BECKER.
*University of Chicago School of Medicine.*

Benign neoplasia of melanoblasts (1) is seen in prenatal pigmented nevi, which are either present at birth or appear during the first few years of life. Human beings average 18 to 20 such lesions (Pack). They vary from small macules to large, elevated, nonhairy or hairy plaques. Most nevi are pigmented; a few small elevated lesions are non-pigmented, especially on the face and scalp.

Acquired nevi appear in late childhood or early adult life in the form of flesh-

colored papules which later become brown (Ebert).

Clinical diagnosis of pigmented nevus is made by dermatologists in 80 to 90% of cases. Of 710 lesions diagnosed as nevi (2), microscopic diagnosis was: nevus in 80%, seborrheic keratosis 5%, papillo-epithelioma 3%, carcinoma 2%, verruca vulgaris 1%, and other diagnoses 9%. Reversing the analysis, of 649 lesions diagnosed microscopically as nevi, nevus had been diagnosed clinically in 87%, seborrheic keratosis 2%, carcinoma 2%, fibroma molle, verruca vulgaris, lentigo maligna, papillo-epithelioma, adenoma sebaceum and cyst, 1% each, and other diagnoses 3%.

Microscopically, nevi are divided into type A (nevus cells in masses associated with the epidermis); B (nevus cells in groups or cords in the dermis); and C (elongated nerve type cells in the deeper dermis). Various combinations of the different types occur. In childhood, types A and AB nevi are most common, in adult life types B and BC predominate. Of 741 specimens of nevi, mostly removed from adults, the classification was as follows (2):

| *Type of Nevus* | *Percentage of Cases* | *Number of Cases* |
|---|---|---|
| A | 2.1 | 16 |
| A and B | 8.7 | 65 |
| B | 16.4 | 122 |
| B and C | 64.3 | 477 |
| A, B and C | 6.6 | 49 |
| C | 1.6 | 12 |
| Total | 99.7 | 741 |

Acquired nevi are of the A and AB types. Because of their activity, they may be confused with lentigo maligna, but may be distinguished from the latter by the fact that the nevus cells only penetrate into the dermis and do not work their way to the surface in the epidermis.

Treatment of nevi depends on the variety, the location and the state of growth. Any nevus which is actually growing or is irritated or inflamed, should be excised surgically. All specimens should be biopsied. If melanoma has supervened, treatment should be carried out for melanoma. Quiescent nevi in sites subject to constant friction should be removed prophylactically. Other nevi are treated for cosmetic reasons. Treatment is carried out by fulguration, electric cautery or solid carbon dioxide. A portion of an elevated nevus should be removed for biopsy, after which treatment is directed toward obtaining a smooth scar. In this way unsuspected degeneration of nevi into melanoma can be kept at an irreducible minimum. Large nevi are excised surgically and replaced by grafted skin.

Malignant neoplasia of melanoblasts (1) usually occurs in form of lentigo maligna, a premalignant or, better, early malignant lesion, starting as an asymptomatic brown macule which enlarges irregularly and becomes slightly elevated. After a few months or years a tumor appears, usually in the center of the plaque, often erythematous (non-pigmented melanoma) or pigmented (pigmented melanoma). In the author's series, melanoma arose as lentigo maligna in 77% of cases, and in true nevi containing nevus cells in only 23%. This contrasts with the statement in most reports that melanoma arises in nevi in more than 50% of instances.

Diagnosis of melanoma is more difficult than that of nevus. Of 76 specimens removed from lesions diagnosed clinically as melanoma, microscopic examination revealed melanoma in only 45%, pigmented nevus and blue nevus each 11%, lentigo 8% and seborrheic keratosis and melanotic basal-celled carcinoma, each 5%. Reversing the analysis—of 59 lesions diagnosed melanoma microscopically, only 51% had been correctly diagnosed clinically. Nevus pigmentosus had been diagnosed in 25%, seborrheic keratosis in 9%, carcinoma in 7% and other diagnoses in 9%. Diagnosis of non-pigmented melanoma is made only by biopsy.

Microscopic diagnosis of lentigo maligna (3, 4, 5) is made by the presence of three features: first, neoplastic proliferation of melanoblasts at the epidermo-dermal junction; second, round cell infiltrate, often pronounced, in the superficial dermis; and, third, sometimes absent, casting off of small masses of neoplastic cells through the epidermis. The cells are ordinarily round or oval, although fusiform melanoma cells are sometimes seen. Microscopic diagnosis of frank melanoma is made by the anaplastic nature of the cells forming the tumor, which may be either round or oval or fusiform. Melanoma originating in a nevus shows malignant neoplasia of melanoblasts at the epidermo-dermal junction. Non-pigmented melanoma is diagnosed by the proliferation of cells at the epidermo-dermal junction with the usual lack of cohesion between the cells, as contrasted to epidermal carcinoma.

Treatment of early lentigo maligna consists of local surgical excision. For later lesions, regional lymph node removal should be strongly considered, and, if a frank melanomatous tumor is present, regional lymph node dissection should be done unless contra-indicated by the presence of extensive metastases.

Prognosis of early melanoma is excellent, but failure to biopsy early lesions and carry out adequate treatment has doomed many persons.

## References.

1. Becker, S. W. and Obermayer, M. E. Modern Dermatology and Syphilology. 2nd ed., Philadelphia, J. B. Lippincott Company, 1947.
2. Becker, S. W. Diagnosis and Treatment of Pigmented Nevi. *Arch. Dermat. & Syph.*, 60:44 (July), 1949.
3. Becker, S. W. Cutaneous Melanoma. *Arch. Dermat. & Syph.*, 21:818 (May), 1930.

4. Becker, S. W. Melanotic Neoplasms of the Skin. *Amer. J. Cancer*, 22:17 (Sept.), 1934.
5. Becker, S. W. Dermatological Investigations of Melanin Pigmentation. The Biology of Melanomas, New York Academy of Sciences, 1948.

Discussion by H. Z. Lund, Western Reserve University, Cleveland, O.

The contrast of appearance of a pigmented nevus of a child and that of an adult is generally known. We have recently made a systematic study of the appearance of benign pigmented nevi at all ages and find that there are, in most instances, progressive changes which roughly correlate with the age of the patient. The most important variables are junctional proliferation which is present to a moderate to marked degree in about 90 per cent. of children under 10 years of age. The subsequent decades show a marked diminution in this percentage but there is no age at which it abruptly ceases. Slight degrees can be found in many nevi in adult life. Mitotic figures are found rarely but likewise show a higher incidence in the first decade and then a steady drop. Mitotic figures are uncommon in adult life. In later life the nevus cells are more fusiform and associated with fibrils. Fibrils progressively increase with age, as do the structures resembling tactile corpuscles. Thus the nevus cells which early in life resemble epithelium gradually differentiate to tissue resembling neuroid structures. There are exceptions to the above trend which cannot be discussed here.

**Reference.**

Lund, H. Z. and Stobbe, G.D. *Am. J. Path.*, 25:1117, 1949.

Discussion by Eugene F. Traub, New York Medical College.

I am in accord with Dr. Becker that an accurate diagnosis of pigmented nevi is possible only after microscopic examination. Not only are a number of other lesions frequently mistaken for pigmented nevi but the differentiation of one pigmented nevus from the other is often impossible without microscopic examination. Dr. Becker has used a classification for the study of nevi based upon that of Miescher and von Albertini. It is not entirely clear to me just exactly what all may be included in each of his three types. Furthermore, to remember them as types "A," "B" and "C," is rather meaningless unless fully explained by the accompanying text or a specially appended name. But it would seem that each of his types may be a hodge-podge of several varieties of nevi, which is never good. For example, type "A" is exemplified by lesions of an intra-epithelial growth while type "B" includes the "common mole" or intra-dermal nevus of my classification as well as the blue nevus and one would have to specify which of these, or any mixed types, was meant. Dr. Becker admits that depending on where and how the sections are cut, one might find the lesion fitting into type "A," "B" or even "C." This would not occur in a classification like mine, except in the case of a mixed nevus as, in most instances, there would be no difficulty in recognizing at once if its exact type is intra-epidermal, intra-dermal, junction or blue nevus.

I do not agree with some of the methods of the treatment suggested by Dr. Becker. He suggests that large macular pigmented nevi could be destroyed with solid carbon dioxide, electrocoagulation or by fulguration. I believe some of these procedures are satisfactory for some of the rather small lesions but where larger pigmented nevi are involved, I believe the hair line scar of a surgical excision gives a better cosmetic result than can be accomplished by making a scar of the entire area. This is particularly true with those nevi complicated with hair that requires extensive electrolysis after the pigment is first destroyed with either solid carbon dioxide, electrocoagulation or fulguration. In these cases, it is much simpler to excise the lesion at one sitting, unless it is so large that closure is utterly impossible and even then sometimes skin grafting is preferable to many repeated treatements by electrocoagulation, electrolysis, etc. Furthermore, as Dr. Becker pointed out, diagnostic errors can only be prevented or corrected on study of the tissues and this can best be done only by excising and examining the entire lesion.

## The Problem of Acanthosis Nigricans.

Helen Ollendorff Curth.
*College of Physicians and Surgeons, Columbia University, New York.*

Acanthosis nigricans is a benign dermatosis showing hyperpigmentation, mostly in the basal cell layer, as well as other characteristic epidermal changes. Warts and pigmented spots or moles may accompany these lesions. About 450 cases of the disease have been reported. The dermatosis is regionally and symmetrically distributed, the axillas being the most commonly involved area. Melanomas do not develop from the lesions. Acanthosis nigricans occurs in man and dog and is found in both sexes. Its significance lies in its association with internal cancer. This combination is seen in 50% of cases of acanthosis nigricans. The type of acanthosis nigricans associated with internal

cancer is falsely called malignant. The type of the disease not so associated is called benign. The two types look alike but can, I believe, be differentiated by careful analysis.

The cancers associated with acanthosis nigricans are highly malignant, non-pigmented adenocarcinomas originating in the stomach or other abdominal organs in 92%, and in the breast, lung, etc., in 8%. Not a single patient has been cured by treatment of the cancer. The cancers occur mostly in the middle-aged but also in the very young and very old. Acanthosis nigricans may precede the cancer by many years, may start simultaneously with, or it may follow cancer. It appears, therefore, that neither acanthosis nigricans nor cancer causes the other. An activating influence of cancer on acanthosis nigricans, however, cannot be denied.

Acanthosis nigricans not associated with cancer may assume the form of a unilateral pigmented verrucous nevus. It starts at birth, in childhood or at puberty. Sex hormones seem to have a stimulating influence on this benign type of the disease. As in the case of melanoma or certain physiological pigmentations, these patients are subjected at puberty to a physiologic barrage of sex hormones which result in hyperpigmentation and other epithelial changes. Studies of the 17 keto-steroids in young and middle-aged men and women suffering from acanthosis nigricans gave normal values. The parallel action of the cancer agent and the sex hormones on the two types of the dermatosis seems noteworthy.

If an individual develops acanthosis nigricans after puberty he will sooner or later show an internal cancer and the cutaneous disease will become more intense with the manifestation of cancer. Young people, however, may have "malignant" acanthosis nigricans before puberty.

Treatment of the malignant type consists in early recognition and removal of the tumor. In the benign type the lesions sometimes regress spontaneously after puberty.

When it was found that there were no recorded familial cases of the malignant type of acanthosis nigricans, such as had been found in the benign type, an investigation of the genetics of the disease under the auspices of the American Cancer Society was undertaken. Furthermore, in this study an effort is being made to determine whether adenocarcinoma occurs in a higher percentage in the families of patients with acanthosis nigricans than in the ordinary population. Particular difficulties were encountered. In addition to all the known handicaps of genetic studies of cancer in man, one cannot be certain whether cancer victims in the older generations had also shown the cutaneous changes, possibly to a mild degree. If the individual has not yet reached puberty or cancer age, acanthosis nigricans is not likely to be noted. Are genetic carriers of the dermatosis those with a great number of pigmented moles, and what is the "normal" amount of moles? Genetic carriers of cancer may not have been recognized because family members were not examined for any special metabolic feature on which cancer associated with acanthosis nigricans might be based. Those who transmit the disease might have exhibited such a disturbance to a lesser degree than patients with overt manifestations.

If we should succeed in establishing malignant acanthosis nigricans as a separate disease, a dermatosis might emerge which would, not in 50% but in 100% of cases, be an indicator of internal cancer and might point the way to the biology of certain malignant tumors.

## Bibliography.

Curth, Helen Ollendorff. Benign Type of Acanthosis Nigricans: Etiology. *Arch. Dermat. & Syph.*, 34:353-366 (Sept.), 1936.

———— Cancer Associated with Acanthosis Nigricans. Review of literature and report of a case of acanthosis nigricans with cancer of the breast. *Arch. of Surgery*, 47: 517-552 (Dec.), 1943.

———— Acanthosis Nigricans and its Association with Cancer. *Arch. Dermat. & Syph.*, 57:158-170 (Feb.), 1948.

———— Acanthosis Nigricans und Krebs. *Z. f. Krebsforschung*, 56:307-328, 1949.

Curth, Helen Ollendorff and Slanetz, C. A. Acanthosis Nigricans and Cancer of the Liver in a Dog. *Am. J. Cancer*, 37:216-223, 1939.

# The Junction Nevus, Forerunner of the Malignant Melanoma and Its Differential Diagnosis from the Standpoint of the Dermatologist.

Eugene F. Traub.

*New York Medical College.*

The pigmented hairy and warty nevi have always been difficult to classify and no logical clinical classification has ever appeared feasible. Therefore, a simple anatomic basis on which to classify them has given us the best chance to simply describe these lesions and to gain definite knowledge as to which of them are potentially dangerous and which generally remain benign throughout their

entire course. We have therefore classified the pigmented hairy and warty nevi as

1. Intra-epidermal Nevi
2. Junction Nevi
3. Intradermal Nevi
4. Blue Nevi
5. Mixed types

The name "junction" was derived from the fact that the cells constituting this nevus arise at the epidermal-dermal junction. Of the group this is the only one which may give rise to a malignant melanoma or nevocarcinoma. Clinically, however, any of the above types may resemble the junction nevus so closely in clinical appearance that only on microscopic examination can one be certain of the diagnosis.

The mixed lesions are particularly confusing because they comprise combinations of any of the above types and generally this can only be recognized on microscopic examination.

Classically the junction nevus is usually small in size, not over 2-3 cm. as a rule, slightly elevated and smooth surfaced. Occasionally the surface may be soft, warty, or uneven, but it never is a hard warty lesion. The color may vary from light brown to brownish-black, or it may even be blue-black. Hairs are not present except in exceptional cases.

Junction nevi may appear at any time in life or may be present at birth. Clinically and microscopically they are indistinguishable regardless of the time of their appearance, but their behavior and prognosis is different. Those present from earliest infancy as a rule grow slowly or not at all, and if they become nevocarcinomas they metastasize more slowly and prognosis following radical treatment is successful in a relatively high percentage of cases. Those appearing in adult life, after puberty, grow more rapidly, metastasize more promptly and the outlook in these cases is always extremely grave. The percentage of cures is low in this group.

Since junction nevi, like all other nevi, are not more prone to cancer development than normal skin, most of these lesions can and should be left alone. Only when they are located at sites of extreme trauma, hands and feet, etc., is it safer to remove them prophylactically. Such removal may be accomplished with the sacrifice of a minimum of surrounding normal skin. This is ample in most cases but if early changes to nevocarcinoma are found, a wider excision may then be deemed advisable.

It should be emphasized that junction nevi are benign and that adequate removal is a perfectly safe procedure without danger of aggravating the local lesion or causing metastasis. It is because of believing that a lesion is benign, when actually it is already malignant, that trouble results from a removal predicated on this erroneous basis. Even then the error can be corrected following microscopic examination of the tissue.

The danger of malignant melanoma or nevocarcinoma can be greatly minimized by the early removal of questionable or badly located junction nevi. To advise removal of all of them is ridiculous. but it is equally bad and far more dangerous to suggest leaving them all alone. We should continually stress that the highest percentage of cures results from prophylactic removal of the earliest lesions.

There are two types of pigmented nevi most likely to be confused with the junction nevus. The first is the benign pigmented intra-epidermal nevus and the second the blue nevus. Less frequently, even the intra-dermal nevus may be confused with the junction nevus. The reason the pigmented intra-epidermal nevus is so frequently confused is because it is a smooth pigmented area devoid of hairs but often with deep black pigment and when located on the hands and feet, where thickness or elevation are difficult to make out, it is almost impossible to be certain whether the lesion is an intra-epidermal or junction nevus. The junction nevus usually shows some thickening but in certain areas this is not easily determined. This point was brought home to me recently by a patient who had about 60 small pigmented nevi on his trunk and extremities. One on the foot was removed and proved to be an intra-epidermal nevus while a similar mark on the back proved to be a junction nevus. Therefore, probably all of the others, not removed, and scattered over his body, belonged in one of these two categories and one would have had to remove each one individually to be certain of its exact type. Would it be advisable to treat indiscriminately all of these nevi with solid carbon dioxide, electrocoagulation, desiccation, etc? It is only fair to state that our rare instances of the development of malignant melanoma or nevocarcinoma following inadequate destruction of junction nevi have resulted from this practice.

The typical blue nevus, because of its blue-black color, can usually be differentiated clinically from the junction type but if the blue nevus is more brownish or brownish-black in color and rather superficially located in the cutis, confusion does frequently result. The benign pigmented intra-epidermal nevus does not terminate as nevocarcinoma or malignant melanoma but in rare instances it has terminated as a carcinoma.

### Bibliography.


Traub, Eugene F. The Pigmented, Hairy and Warty Nevi and Their Relationship to Malignancy. *Southern Med. Jour.*, 40 (12): 1000-1005, Dec., 1947.

——— Early Recognition of Possibly Dangerous Nevi (Moles) and the Best Procedure to Avoid Development of Malignant Melanomas (Nevocarcinoma). *N. Y. State Jour. Med.*, 49 (14): 1661-1664, July 15, 1949.

——— The "Common Mole." Its Clinicopathologic Relations and the Question of Malignant Degeneration. *Arch. Dermat. & Syph.*, 41: 214-249, Feb., 1940.

——— Congenital Anomalies (Nevi) and Their Relationship to Cancer and Melanoma. *Penn. Med. Jour.*, pp. 1-8, June, 1941.

Discussion by H. Z. Lund, Western Reserve University, Cleveland, O.

From the standpoint of the surgical pathologist, recognition of early melanoblastoma and distinction from benign nevus are extremely important. The first feature which is looked for is junctional proliferation because most, if not all, melanoblastomas arise in the epidermis or at the dermo-epidermal junction. Traub and Keil have stressed this and awakened many to awareness of it. However, the emphasis has been insufficiently critical and there has been an acceptance by some dermatologists and pathologists that the presence of junctional proliferation at any age and of any degree is evidence of a potentially malignant lesion. Such a conclusion is drawn from the article by Traub and Keil. Actually the feature of junctional proliferation becomes significant if it is unusual in degree for a given age, as, for example, the finding of a nevus of a middle-aged person which has the histological characteristics of a nevus of childhood; i.e., the cells are largely junctional in distribution, resemble epithelium and there is little evidence of differentiation to ordinary nevus cells and cells associated with fibrils. Such an appearance leads to the suspicion that the lesion is incipient and growing. (The clinical evidence obtained in our own analysis of the duration of growth of such lesions was variable and conflicting, permitting no final conclusion. Additional study is needed.) The pathologist is to be guarded in excluding melanoblastoma in these cases, but until more conclusive evidence is obtained, a positive diagnosis must rest on this finding plus additional changes, including (a) excessively large, irregularly scattered or otherwise bizarre masses or nests of cells at the dermo-epidermal junction, (b) deep penetration of large cells without differentiation to small nevus cells and fibrillar forms, (c) more mitotic figures than are usual, (d) atypical and pleomorphic cells, (e) invasion, (f) trophic changes, and (g) inflammation, other than folliculitis, which is not accounted for by trauma.

References.

1. Traub, E. F. and Keil, H. The "common mole," its clinicopathologic relations and the question of malignant degeneration. *Arch. Dermat. & Syph.*, 41, 214-252, 1940.
2. Lund, H. Z. and Stobbe, G. D. The natural history of the pigmented nevus; factors of age and anatomic location. *Am. J. Path.*, 25:1117, 1949.

Discussion by S. William Becker, University of Chicago School of Medicine.

The term "junction nevus" has been criticized because such designation includes both "A" and "AB" nevi, for which it could be legitimately used, and, in addition, the obligative premalignant (or actually malignant, depending on the criteria used) disorder called "lentigo maligna" by Dubreuilh. My preference is to designate as pigmented nevi only those lesions composed of benign melanoblastic cells (nevus cells).

Dr. Traub has again emphasized the necessity for microscopic examination of nevi and tumors with which they may be confused. He has shown with excellent colored photographs, a "junction nevus" and an "intraepidermal nevus" which cannot be distinguished clinically. On the basis of his excellent colored photomicrographic slides of the two disorders, it would seem that the first satisfies fully all the requirements of "lentigo maligna" of Dubreuilh. The second is composed entirely of epithelial cells and contains no neoplastic melanoblasts, and would seem to belong in the group of benign epidermal neoplasms (Becker, S. W.: Benign Epidermal Neoplasms, Arch. Dermat. and Syph., 26:838 (Nov.) 1932) and could be called "benign epithelioma."

At any rate, it seems more scientific to classify pathologically rather than to perpetuate the older designation "nevus" in the sense of a "mark."

## The Development of Epidermal Pigmentation in the Negro Fetus.

Arnold A. Zimmermann.

*Department of Anatomy, University of Illinois, College of Medicine, Chicago, Ill.*

Fetal Negro skin constitutes excellent material for the study of melanogenesis. Surprisingly, no systematic survey, throughout the fetal stages, had previously been made. The main advantages reside primarily in the high potentiality for melanin production of specialized cells which reveal their activity early in fetal life. They are the dendritic melanoblasts which remain distinct, both morphologically and functionally, from ordinary epithelial cells. They are the sole producers of melanin both in the epidermis and in the papillae of hair follicles. The distribution and signficance of dendritic cells in the adult human skin, both white and pigmented, recently was studied by Billingham.

The derivation of mammalian melanoblasts from the neural crest has been demonstrated by Rawles (1947). In the fetal Negro

skin, however, the search for migratory melanoblasts in the dermis, previous to their identification in the epidermis, encounters difficulties. If potential melanoblasts are present in the embryonic or early fetal dermis they cannot be demonstrated either by a positive dopa-reaction or by the usual silver techniques. This might be due to insufficient amounts of a melanogenous substrate (tyrosine) or to incomplete, as yet inactivated oxidizing enzyme-systems in the precursors of epidermal melanoblasts. The latter assumption appears more probable. Experimental evidence in Amphibia has established the fact that the ectoderm plays an important role in melanin formation (DuShane, 1943). My observations in the fetal Negro skin, so far, appear to confirm the hypothesis that substances necessary for the synthesis of melanin may be supplied by epidermal cells. An appositional relationship of human melanoblasts to the epidermis seems to be essential for their full functional activity. The material for this histological study of fetal Negro skin consisted of skin-specimens from 75 abortions. The main results may be summarized as follows:

1. The basal cells of the human epidermis do not produce melanin.

2. The true source of melanin resides solely in the pigmentary dendritic cells or melanoblasts which constitute an independent cell-type within the epidermis.

3. Dendritic melanoblasts first appear in the fetal Negro skin early in the third month.

4. There are no cytological or functional transitions between epidermal melanoblasts and ordinary epithelial cells.

5. The dendritic melanoblasts consistently show a positive dopa-reaction throughout fetal life. Basal and other epidermal cells remain dopa-negative.

6. Dendritic melanoblasts of the third fetal month contain melanin-precursors (premelanin) which can be demonstrated by reduced silver methods. From the fourth fetal month to term they contain both premelanin and melanin granules.

7. The earliest melanoblasts in the epidermis have ovoid, fusiform or stellate cell-bodies with few and short dendritic processes at their poles. In the fourth fetal month the total length of dendritic melanoblasts may reach 100 microns. Their primary dendritic processes extend through the epidermal intercellular spaces and begin to form an intricate syncytium.

8. During the fifth fetal month numerous secondary dendritic processes arise from the long primary processes of the melanoblasts. These secondary tufts approach and progressively surround the ordinary epithelial cells mainly on their distal pole.

9. In unstained sections, brown melanin granules are first identified within the melanoblasts in the late fourth and early fifth fetal months.

10. The transfer of melanin granules elaborated in the dendritic melanoblasts to neighboring epithelial cells begins late in the fifth fetal month. This process is accentuated throughout the remainder of the fetal period. The transfer occurs mainly from the secondary dendritic processes and leads to the accumulation of melanin in ordinary epidermal cells as "supra-nuclear caps." The active melanoblasts gradually become concealed among the pigment-carrying epithelial cells.

11. Melanization of hair shafts and of the matrix of the papillae in all essentials is similar to that of the epidermis. Dendritic melanoblasts accumulate in the papillae and extend their processes directly into the growing base of hair-shafts, thus melanizing them independently of a pigmented epithelial matrix. The latter receives melanin granules quite secondarily after melanization of the hair shaft is well under way.

References.


1. Zimmermann, Arnold A. The development of epidermal pigmentation in the Negro fetus. *Anat. Rec.*, 100, p. 96, April, 1948.
2. Zimmermann, Arnold and Th. Cornbleet. The development of epidermal pigmentation in the Negro fetus. *Journ. Investig. Dermatol.*, 11, pp. 383-392, Nov., 1948.
3. Rawles, Mary E. Origin of pigment cells from the neural crest in the mouse embryo. *Physiol. Zool.*, 20, 248-266, 1947.
4. ——— Origin of melanophores and their role in development of color patterns in Vertebrates. *Physiol. Rev.*, 28, 383-408, 1948.
5. DuShane, Graham P. The embryology of Vertebrate pigment cells. Part I. Amphibia. *Quart. Rev. Biol.*, 18, 109-127, 1943.
6. Billingham, R. E. Dendritic cells. *Journ. Anat.*, 82, 93-109, April, 1948.
7. ——— Dendritic cells in pigmented human skin. *Journ. Anat.*, 83, 109-115, 1949.


Discussion by Hermann Pinkus, Wayne University Medical College, Detroit, Mich.

Dr. Zimmermann in his splendid investigation was unable to find evidence of multiplication of fetal melanoblasts. Masson (The Biology of Melanomas, 1948, p. 31 and plate 15, fig. 1) has stated his belief that epidermal melanoblasts usually multiply by amitosis, but says that he saw one unquestionable mitosis. I would like to contribute the purely accidental observation of mitotic division of normal dendritic pigment cells in the basal layer of adult human skin. (Pinkus, H.: Mitotic Division of Human Dendritic Melanoblasts, *J. Investig. Dermat.*, 13: 309-311, Dec., 1949). The specimen was a common wart (verruca vulgaris) taken from the finger of a dark colored woman. Two unquestionable and two suggestive instances of mitosis were seen in twenty-four routine histologic sections. Mitosis of Malpighian cells was common in this specimen. Without doing an actual count, it was my impression that the ratio of dividing and resting nuclei was similar for dendritic and Malpighian cells.

This experience proves that human melanoblasts can multiply by mitosis in non-malignant conditions. I have also recently observed occasional instances of mitosis of benign nevus cells in ordinary papillomatous nevi.

## A Comparative Study of Malignant Melanoma Among Negro and White Patients.

RUDOLPH J. MUELLING, JR. & WALTER J. BURDETTE.

*Departments of Pathology and Surgery, Louisiana State University School of Medicine, New Orleans, La.*

The admissions to Charity Hospital of Louisiana at New Orleans are nearly equal for white and Negro males and females. During the period from 1937 to date, there have been 101 cases of malignant melanoma among 26,800 malignant tumors in 686,293 admissions. That is, approximately 4 cases of malignant melanoma occurred per 1,000 cases of malignancy.

Approximately one-third (32%) of these melanomas occurred in Negro and two-thirds in white patients. The sex incidence in the Negro group was equal, whereas the incidence in white females was slightly higher than in white males. The majority of cases (88%) occurred between the ages of 30 and 80 years, those in Negroes having highest incidence some ten years later than those in white persons.

The foot was the most common site for the primary lesion in the Negro (50%) while in the white race the trunk was most common (33%). A pre-existing mole was described in one-third of the cases, mostly white. A history of trauma was elicited in one-half of the Negroes and one-tenth of the white patients. It is not possible to tell how much of the trauma was coincidental and falls in the *post hoc, ergo propter hoc* class. Clinical evidence of regional lymph node metastasis was found in about one-half of the cases. Better results of therapy were obtained when it was administered in the hospital rather than as hospital outpatients or in a physician's office and when the metastases as well as the primary lesions were included in the plan of treatment. Inadequate excision with recurrence of the primary lesion was recorded in 17 cases. Two cases of melanoma appearing during pregnancy were found to be of anaplastic histological appearance and were fatally terminated in a short time. The mean duration of life was 4 years and 5 months for the entire group. Eighteen out of 42 patients had a family history of at least one other individual with cancer. None of these had melanoma, however.

The sex incidence of malignant melanomas found is in agreement with that reported by Pack and co-workers (8) in an analysis of 862 cases. Dawson also found a history of the presence of a mole in one-third of the cases. However Pack et al (8) and Broders and MacCarthy (4) record this finding in one-half of their cases. Perhaps this discrepancy may be explained by the low incidence of antecedent moles among Negroes. The incidence of concomitant trauma is similar to that given by Pack et al (8) but much lower than that given by Horwitz (5), 57%. The tumor may arise from any portion of the Negro's skin or eye as Sutton and Mallia (10) have reported. However, when the lesion occurs, it is more apt to arise in the less pigmented areas of the body, such as the foot (7). The individuals in which they appeared were not all lightly pigmented but in many instances were exceedingly dark. The rapidity of the process in two Negro males followed to termination demonstrates that de Lignis' (6) conclusion that malignant melanoma in the native of Northern Transvaal is a less intense process does not always hold true for the Negro in America. The evidence given here would indicate that the American Negro is not as peculiarly immune to malignant melanoma as one might assume from the literature. (1, 2, 3).

### SUMMARY.

1. Malignant melanoma was approximately one-half as frequent in Negroes as in white persons in a population of patients equally divided as to race and sex. This is a higher incidence than that usually quoted for Negroes.

2. Malignant melanomas arose more frequently from a mole in white than in Negro patients.

3. Metastases to regional lymph nodes occurred frequently.

4. Early therapy is better performed by those capable of treating not only the primary but also secondary lesion.

### BIBLIOGRAPHY.

1. BAUER, J. T. Malignant melanotic tumors in the Negro. *Bull. Ayer Clin. Lab. & Pa. Hosp.*, 10:5-11, 1925.
2. BECKER, W. Cutaneous melanoma. *Arch. Dermat. & Syph.*, 21:818-835, 1930.
3. BISHOP, E. L. Melanoma in the Negro. *Am. Jour. Cancer*, 16:522-539, 1932.
4. BRODERS, A. C. and MACCARTHY, W. C. Melano-epithelioma. *Surg., Gyn., & Obstet.*, 23:28-32, 1916.

5. HORWITZ, A. Melanotic tumors. *Ann. Surg.*, 87:917-933, 1928.
6. DE LIGNIS, M. J. H. Tumors in North Transvaal. *S. African Med. Jour.*, 1:102-107, 1927.
7. MUELLING, R. J. Malignant melanoma. *The Military Surgeon*, 103:359-364, 1948.
8. PACK, G. T., PERZIK, S. L. and SCHARNAGEL, I. M. The treatment of malignant melanoma, report of 862 cases. *Cal. Med.*, 66: 283-287, 1947.
9. SPENCER, N. A. Melanoma. *Brit. Med. Jour.*, 2:907-913, 1923.
10. SUTTON, L. A. and MALLIA, W. M. Malignant melanoma in the Negro. *Arch. Dermat. & Syph.*, 8:325-343, 1923.

## *Second Session: Genetical.*

### Introduction.

W. E. HESTON.

*National Cancer Institute, Bethesda, Md.*

Since the birth of his science at the turn of the century, the geneticist has had a profound interest in pigment. Color variations readily attracted his attention. It was through the study of coat color characters in mice and other rodents, plumage color in the fowl and eye color in *Drosophila* that much of the basic information on gene segregation, linkage, sex-linked characters, etc., was derived.

In his book on the Genetics of the Mouse, Grüneberg lists coat color genes located at 10 different loci, and two series have 5 alleles each. To this list could be added several more recently discovered coat color mutants as well as three genes controlling distribution of pigmented areas. Analyses of these characters by Cuenot, Little, Castle, Morgan, Dunn and others constituted a major portion of the mammalian genetics of the first quarter of the century.

Beyond the study directed at the gene itself, the geneticist is next interested in linking the gene to the biological character. He wants to analyze the physiological and biochemical steps between the primary gene action and the end result. Here again the study of pigment has offered especial advantages as emphasized by the work of those reporting at this conference and of others, particularly Beadle and Ephrusi, and Wright and his students. As compared to other gene action paths those concerned with color appear to be relatively simple. Furthermore the processes occur in cells readily accessible, and the history of these processes may be accurately recorded in such structures as the hair or feathers.

It is in studies such as these that the geneticist meets face to face with the biochemist, for final analysis of the gene action paths is on the biochemistry level. On the other hand the geneticist can be of great aid to the biochemist for already the geneticist has identified many of the genes related to the enzymes involved.

The pigmented tumors afford a special field of physiological genetics. Those in the fruit fly and the platyfish hybrids have been of particular value because of the adaptability of both organisms to genetic and cytologic analysis and also because of the vast knowledge of the genetics of both organisms but particularly of the fruit fly. Along with the physiology of pigment formation is that of the malignant transformation, thus presenting a picture in which there is some danger in confusing the two sets of processes. Are the genes which are responsible for the presence of the pigment cell, also in part at least responsible for the abnormal growth of the cell, or is the inheritance of the pigment cell more in line with that of eye and hair color, and the inheritance of the control of the growth of the cell in line with the genetics of neoplasms derived from other types of cells? In either case, what are the processes involved? As will be indicated in the reports of this section, much progress has been made in answering the basic questions in these fields of physiological genetics.

### REFERENCE.

HESTON, W. E. Genetics of Cancer. Advances in Genetics. 2:99-125, 1948.

### Significance of Quantitative Histological Studies of Pigment Found in the Coat Color Mutants of the Mouse to Questions of Normal and Atypical Cell Growth.

ELIZABETH SHULL RUSSELL.

*Roscoe B. Jackson Memorial Laboratory, Bar Harbor, Me.*

Differences in visual effect of pigments in mouse hair are determined by variations in seven attributes of the melanin granules deposited there. Quantitative histological studies have shown four key pigmentation characteristics, relatively independent of

each other. From tip to base each hair is the final record of a regulated series of events occurring at each moult in the pigment-forming cells of the hair follicle. Variations must be due to differences in number structure, or behavior of melanoblasts or possibly, in some cases, to differences in the hair matrix cells receiving the pigment. The stage of hair growth causes non-genetic variations in the complex, degree of pigmentation, involving changes in both number and size of granules, especially apparent in types with moderate or small total amounts of pigment deposition. In these there is a considerable lag in the commencement of pigmentation. Analysis of changes in granule attributes with this pigmentation lag have been very valuable in determining the changes produced by simple quantitative alterations. The major genes affecting coat-color have been shown to affect one or at most two of the key pigmentation characters.

The agouti series controls a trigger mechanism, reversibly shifting the nature of pigment from eumelanin to xanthin. Since eumelanotic and xanthic pigments are chemically different; since eumelanotic granules are extremely variable in size and shape, while xanthic granules are always round; and since under most conditions many more considerably larger granules are deposited in eumelanotic than in corresponding xanthic regions, the differences between the two systems of pigmentation must be quite extensive. Nevertheless, the rapid shift from one type to the other in agoutis suggests, though it does not prove, that the same melanoblasts produce both pigments, the difference being due to an altered condition within the melanoblast or hair matrix cell. Since non-agouti and agouti hairs start pigment formation identically, the agouti series genes definitely do not act by altering the time of arrival or beginning of functioning of melanoblasts.

The action of the albino series is a quantitative change in the degree of pigmentation, affecting all types of pigment. For each qualitatively different type of pigment, its effects closely parallel the effect of pigment lag related to stage of hair growth. The gene action here could be change either in number or in activity of melanoblasts.

Black-brown substitution alters the nature of eumelanotic pigments, but usually not their number. It seems that the *Bb* pair of genes must alter the function of some type of cell, rather than changing number.

Pink-eye substitution alters eumelanotic granule size (*aapp* has tiny irregular shreds) and also degree of pigmentation. The action could be due to a qualitative defect in the sites of pigment deposition or to a great deficiency of some substance essential to eumelanin formation but not to xanthin formation.

The dilute gene causes strong granular clumping which is almost certainly an intercellular affair resulting from altered behavior of melanoblasts. There is no real reduction in amount of pigment, only an extremely irregular arrangement in which ⅓ to ⅔ of all pigment is concentrated into large clumps which absorb little light.

The W-genes appear to alter the top limit of granule number, their effect differing from that of the albino series in that they reduce granule number much more than size. Since the effects of the W-genes on pigment are exactly paralleled by their effects on erythrocyte number and size (a severe macrocytic anemia is produced in the black-eyed white genotypes), and the effects on gonad development are also very similar, it seems probable that this series of genes is able to affect several types of cells. This is in strong contrast to the strict local and follicle-limited action of the other genic series.

Throughout it appears that a given genic substitution alters only one aspect of the pigmentation process. The logical assumption of the physiological geneticist is that the dominant allele usually actively affects a process which is deficient in the presence of the double recessive. If this assumption holds for pigmentation, six different processes have been shown, all of them active in producing the pigment of wild-type mouse hair. A thought I would like to leave with a group studying pigmentation intensively is that since there are at least six independent processes involved in pigment deposition, it is very possible that some of them may affect behavior of melanoblasts, some number of melanoblasts, some the structure and function of cells forming the hair shaft and still others could have to do with a substance diffusing out from the hair papilla.

## Bibliography.


Russell, E. S. A quantitative histological study of the pigment found in the coat color mutants of the house mouse. 1946. I. Variable attributes of the pigment granules. *Genetics*, 31:327-346. 1948. II. Estimates of the total volume of pigment. *Genetics*, 33:228-236. 1949a. III. Interdependence among the variable granule attributes. *Genetics*, 34:133-145. 1949b. IV. The nature of the effects of genic substitution in five major allelic series. *Genetics*, 34:146-166.

———— 1949c. Analysis of pleiotropism at the W-locus in the mouse: Relationship between the effects of *W* and $W^v$ substitution on hair pigmentation and on erythrocytes. *Genetics*, 34:708-723.

## Melanotic Tumors in *Drosophila*.*

WALTER J. BURDETTE.
*Louisiana State University School of Medicine, New Orleans, La.*

At least 24 different strains of *Drosophila* which develop tumors have been described (1). A few, such as *me*, probably represent the end result of a degenerative rather than a neoplastic change (4). All except one of the remainder have tumors which are melanotic. They are usually present in only a portion of the animals, although those without tumors transmit the susceptibility to their progeny. In the 8 stocks we have studied the incidence ranges from less than 1% to 50%. The tumors appear early in larval life and become pigmented. With metamorphosis the cellular elements regress, leaving a residue of pigment by which they are identified grossly. The tumors which we have observed are benign, their characteristic size and location varies from one strain to another, and multiple tumors are not uncommon. They also survive transplantation.

Sections reveal that the tumors are composed of polyhedral cells in clusters and fusiform cells may also be present. The tissue of origin has been inferred from the location and superficial resemblance to adjacent structures, but such conclusions are open to question (6). In the adult, amorphous pigment is all that remains.

These stocks of *Drosophila* have been inbred and isogenic strains isolated. It is possible not only to find the chromosomes responsible for tumor susceptibility in *Drosophila* but also to determine the locations of the genes involved on a specific part of each chromosome in certain instances. The number, location, and action of genes varies among the strains. Also certain tumor genes from one strain may affect tumor susceptibility when introduced into another tumor stock. Genes affecting tumor susceptibility have been found on the X chromosome and the three autosomes. Some modifying genes may enhance susceptibility while others suppress it. A single gene near the left end of the X chromosome is responsible for the *lethal 7* tumor (2). On the other hand, Stark reports that there are genes on four chromosomes affecting tumor incidence in *be-3* (5). The second chromosome is largely responsible for the presence of tumors in $tu^{g}$ and $tu^{48j}$.

The incidence of these melanotic tumors is affected by the environment in which the flies are raised. There are usually fewer tumors when cultures are crowded, and nutrition, temperature, and irradiation also influence the number of tumors which appear. Therefore it is very important to maintain uniform culture conditions when studying the tumors.

We have also used *Drosophila* to investigate chemical mutagens and carcinogens. Reports of the parallelism between carcinogenic and mutagenic properties of certain chemicals has lent support to the hypothesis that mutations play an important role in the etiology of tumors (3). In our laboratory results to date indicate that carcinogens are not always mutagens although they may be in some instances. Methyl-*bis* (betachloroethyl)amine hydrochloride and 20-methylcholanthrene have been administered to flies and tests made for lethal mutations on the X chromosome. Using nitrogen mustard, 149 mutations were found in 17,052 chromosomes tested. Eight parents were responsible for 67 of these lethals which were probably carried over from a previous generation since the material was administered serially. Methylcholanthrene was administered as a vaginal douche and also as an aerosol. There were 3 mutations in 4.660 chromosomes tested in the former and 10 in 10,108 in the latter. Untreated flies showed 2 mutations among 2,822 chromosomes tested. In contrast to the data for nitrogen mustard, these results do not support the idea that methylcholanthrene is a mutagen, although the low mutation rate might be due to strain or species differences in response or to insufficient dosage for the mode of administration.

The use of *Drosophila* as a test animal in the study of atypical growth thus presents certain advantages. This is particularly true for the study of hereditary factors which are active in many and diverse types of neoplastic disease. Both hereditary and environmental factors are relatively easily controlled, the chromosome number is small, the life cycle is short, and the mutation rate may be determined in an objective manner. Experiments with tumors in *Drosophila* may have added significance because of certain similarities to mammalian atypical growth. In this animal we already have concise evidence of gene action in tumor formation, and further study may be equally informative.

* Aided by a grant from the National Cancer Institute, United States Public Health Service.

### REFERENCES.

1. BURDETTE, W. J. Tumors and mutations in *Drosophila*. Texas Reports on Biol. & Med., 1950. In press.
2. BRIDGES, C. B. Non-disjunction as proof of the chromosome theory of heredity. *Genetics*, 1:107-163, 1916.
3. DEMEREC, M. Induction of mutations in *Drosophila* by dibenzanthracene. *Genetics*, 33:337-348, 1948.
4. GOWEN, J. W. The inheritance of focal melanosis in *Drosophila*. *Arch. Path.*, 17:638-647, 1934.
5. STARK, M. B. and BRIDGES, C. B. The linkage relations of a benign tumor in *Drosophila*. *Genetics*, 11:249-266, 1926.
6. RUSSELL, E. S. A comparison of benign and "malignant" tumors in *Drosophila melanogaster*. *J. Exper. Zool.*, 84:363-385, 1940.

## Genetic Pigment Mosaics in the Pigeon.

W. F. HOLLANDER.

*Department of Anatomy, Yale University School of Medicine, New Haven, Conn.*

Plumage pigment of wild-type *Columba livia* is black, but domestic varieties exhibit also such hereditary conditions as "brown" or "chocolate" (recessive, sex-linked), "ash-red" (dominant, sex-linked, allele of brown), "almond" (dominant, sex-linked, closely linked with "brown"), "faded" (dominant, sex-linked, allele of "almond"), "dilute" (recessive, sex-linked), "recessive red" (not sex-linked), "grizzle" (dominant, not sex-linked), and others.

Occasionally striking patchwork or mosaic combinations ("chimeras") of the above color types are found. These afford some opportunity for analysis of pigment physiology. Successive molts produce little alteration in such specimens, and adjacent feathers growing at the same time may differ completely, so that horomonal control does not seem involved. On the other hand, feathers at the edge of such patches may change color at molting, indicating that melanoblasts rather than tissue cells govern the pigmentation and are capable of some migration. There is a perfect analogy here with grafted (experimental) color mosaics. Genetic evidence, from pedigrees and progeny tests, indicates that a number of such specimens may actually be a sort of natural graft, as a result of autonomous tissue formation by supernumerary sperms in embryogenesis. Other cases may have more conventional origins, such as chromosome aberrations, or somatic gene mutation.

Another type of mosaic effect, more commonly observable, is referred to as "flecking" or variegation. This occurs usually in pigeons of the "ash-red," "almond," "faded," and "grizzle" color types. For example, flecks in an ash-red male are black if he is heterozygous for black, but brown if he is heterozygous for brown; flecks in a male almond heterozygous for brown are black, brown, and faded (side by side). Genetic control is very evident. The flecks vary in size from almost microscopic to entire feathers or even small patches of feathers. When large, they usually show a lengthwise orientation in the feather.

Flecks appear to be local somatic "mutations" of the dominant gene involved, so that a recessive allele appears. The effects are apparently much the same as in the "position effect mottling," extensively studied in *Drosophila*. Apparently the "mutations" may occur at any time in the life of a pigment cell, and in the case of extremely small flecks may occur after the final mitosis. Since there is sharp distinction in pigmentation of the flecks, it seems probable that the melanoblast is diploid; mutation in a polyploid cell would probably result in graded changes.

Both chimeric and variegated mosaic effects are known among other domestic birds, and other animals.

Specimens were displayed at the meetings.

### REFERENCES.

HOLLANDER, W. F. Mosaic effects in domestic birds. *Quart. Review Biol.*, 19:285-307, 1944.

———— Bipaternity in pigeons. *Jour. of Heredity*, 40:271-277, 1949.

Discussion by J. P. TRINKAUS, Osborn Zoological Laboratory, Yale University, New Haven, Conn.

*Role of Epidermis and Hormones in the Differentiation of Melanoblasts.*

The melanin pigments of feathers are deposited in the epidermal cells of the differentiating feather by branched pigment cells called *melanophores*. In the undifferentiated condition, prior to the synthesis of pigment granules, they are referred to as *melanoblasts*. In the Brown Leghorn fowl, grafting experiments have demonstrated that the melanoblasts are embryonic-type cells, in feather germs of the adult as well as of the embryo, with a dual potency; they may form either black or red melanophores [Trinkaus, *J. Exp. Zool.*, 109:135-170 (1948)]. The differentiation of melanoblasts, within the limits set by their genic constitution, is markedly influenced by the tract-specific epidermis of each feather germ, and by estrogenic and thyroid hormone [Trinkaus, *J. Exp. Zool.*, 113, in press (1950)]. The nature of the resulting pigment pattern in each feather is, therefore, a consequence of the complex interaction of a number of tissue and humoral factors [cf. review by Rawles, *Physiol. Rev.*, 28:383-408 (1948), for studies on pigment patterns in other fowl, and in amphibians and mammals].

This analysis suggests, of course, that more attention might be directed to the possible role of tissue and humoral factors, in other studies on the differentiation of normal and atypical pigment cells. It would be of interest, for example, to determine whether the pigment mosaics in pigeon feathers, described by Dr. Hollander, are due to modifications of the melanoblasts, or of the epidermis (or of both). By grafting melanoblasts from the pigmented area of a regenerating mosaic feather to the wing bud of an embryo, the melanoblasts would differentiate in the presence of different epidermis. The nature of the resulting pigment pattern in the host wing feathers should give a critical answer to the question.

## Pigment Formation in the Eye of *Ephestia* and Its Genic Determination.

ERNST CASPARI.

*Wesleyan University, Middletown, Conn.*

In the study of the eye pigments of the meal moth *Ephestia*, the integration of embryological, biochemical and genetic analysis has proceeded so far as to give a consistent picture of the interaction of these factors. Pigments occur in three types of cells, primary pigment cells, accessory pigment cells, and retinula cells. The pigment in the latter two types of cells is deposited in small brown granules insoluble in water, while a yellow, water-soluble pigment is found in the primary pigment cells.

The chemical behavior of these pigments is known from the investigations of Becker (1942). The brown pigment is a substance with well-defined chemical characteristics different from melanin, which has been given the name "skotommin." Skotommin is derived from tryptophane according to the scheme: Tryptophane → kynurenin → oxykynurenin → pigment.

Developmentally, pigment appears first in the retinula cells. Pigment formation starts in these cells in the prepupa, and spreads gradually over the eye in the first 9 days of pupal life. Pigment appears in the accessory pigment cells about 10 days after pupation, in the primary pigment cells a few days later. Pigment formation in the accessory pigment cells has been more thoroughly described by Hanser (1948). The first thing to appear are very small precursor granules which enlarge under deposition of pigment on their surface. These precursor granules persist as the core of the final pigment granule. By enzymatic digestion experiments it could be demonstrated that the precursor granules contain ribonucleoproteins (Caspari and Richards, 1948).

Two genes affecting the pigmentation of the eye have been studied, *a* and *wa*. *a* interferes with the transformation of tryptophane to kynurenin, and in this way reduces the amount of skotommin pigment by 80-90%. The size of pigment granules is decreased. *wa* inhibits the formation of pigment completely, but does not interfere with the production of kynurenin. Hanser found that in *wa wa* animals the precursor granules are not formed.

*aa* animals can form large amounts of skotommin if supplied with kynurenin either by transplantation of wild type organs (Caspari, 1933) or by injection. In this way it can be shown that the different types of cells of the eye have different "sensitive periods" in which they are competent to react on supply of kynurenin with pigment formation (Hanser, 1948). These sensitive periods start somewhat earlier than the periods in which pigment formation can be observed, and continue through the time of visible pigment formation. In accessory pigment cells, the sensitive period seems to start at about the time when the precursor granules become visible.

From these experiments the following picture of pigment formation arises. For the formation of pigment granules, at least two conditions are necessary: the presence of kynurenin, the chemical precursor of the pigment, and the ribonucleoprotein containing granules. While the latter are not necessary for the formation of kynurenin, they probably have some function in transforming it into the pigment. Kynurenin is formed throughout the larval and pupal stages in all organs investigated (Caspari, 1949). Different cells acquire at different stages of their development the ability to react on kynurenin supply with formation of pigment. This stage of competence seems to be correlated with the appearance of the precursor granules, and forms the developmental basis of the sensitive period. Genes may interact with pigment formation by affecting either kynurenin formation (*a*) or the formation of precursor granules (*wa*).

### BIBLIOGRAPHY.

BECKER, E. Uber Eigenschaften, Verbreitung und die genetisch-entwicklungsphysiologische Bedeutung der Pigmente der Ommatin-und Ommingruppe (Ommochrome) bei den Arthropoden. *Z. ind. Abst.-Vererb.*, 80:157-204, 1942.

CASPARI, E. Uber die Wirkung eines pleiotropen Gens bei der Mehlmotte *Ephestia kühniella* Z. *Arch. Entwmech. Org.*, 130:253-281, 1933.

——— Physiological action of eye color mutants in the moths *Ephestia kühniella* and *Ptychopoda seriata*. *Quart. Rev. Biol.*, 24:185-199, 1949.

——— and J. RICHARDS. Genic action. Yb. Carnegie Inst. Wash., 47:183-189, 1948.

HANSER, G. Uber die Histogenese der Augenpigmentgranula bei verschiedenen Rassen von *Ephestia kühniella* Z. und *Ptychopoda seriata* Schrk. *Z. ind. Abst.-Vererb.*, 82:74-97, 1948.

## Problems of Origin and Migration of Pigment Cells in Fish.

H. B. GOODRICH.

*Wesleyan University, Middletown, Conn.*

In two papers published in 1915 Charles Stockard observed the origin of yolk sac chromatophores in *Fundulus* from chromatoblasts which migrated from the region of the closure of the blastopore and from the

side of the embryo. In the light of the more recent "fate" maps of teleosts, these cells migrating from the blastopore would probably be considered to have come from the presumptive mesodermal region of the germ ring. There does not at present appear to be available critical evidence to demonstrate the origin of fish chromatophores from the neural crest as in amphibia, birds and mammals. Transplants by Oppenheimer (1938) from the germ ring 180° removed from the embryonic shield gave rise to chromatophores. Hybridization experiments (by Goodrich, unpublished) between *Fundulus* and *Oryzias* yielded some embryos without neural plate but with abundant chromatophores on the yolk sac. Lopashov's (1944) experiments on later stages may indicate an origin of chromatophores from the neural region. It seems not unlikely, however, that yolk sac chromatophores in the teleost may arise from remnants of the germ ring in the region of the closing blastopore.

Other problems of pigmentation involve the determination of various cell types such as the melanophores, xanthophores and iridocytes. Also sharply differentiated types of melanophores have been described as existing in the same fish *(Platypoecilus, Oryzias)*. Evidence seems to indicate that all such cell types are determined prior to arrival in their final location.

Patterns may for convenience be classified under micro-patterns and macro-patterns. The micro-patterns have to do with the spacing and arrangements of cells observable only under the microscope. In many cases there is a uniform distribution of cells over large areas. There is evidence, especially from the goldfish, *Carassius auratus* (Goodrich and Anderson, 1939), of the existence in the dermis of a reservoir of chromatoblasts. Unpublished observations by Goodrich on *Xiphophorus hellerii* have traced the history of individual cells over a period of nine months. As cells disintegrate others appear in their places. In the variety of goldfish known as the Shubunkin, clusters of new melanophores erupt from time to time irregularly over the surface of the body. There may, however, occur a period of general lysis of melanophores over large areas. After this no further cells arise in the affected areas. Apparently the reservoir of chromatoblasts has also been destroyed. Formation of such clusters may be stimulated by radiation with ultra-violet light (Goodrich and Trinkaus, 1939), but this can not be accomplished after such a period of lysis. Nevertheless, such areas are not after such a period of destruction unfavorable for the existence of melanophores as they may be transplanted into these regions (Goodrich and Nichols, I, 1933). Cells in micro-patterns are often clustered. It is not known whether this is a phenomenon of aggregation or of common origin by cell division as in the Shubunkin.

The macro-patterns are those seen without magnification. Sometimes patterns arise as in the goldfish by destruction of some of the cells in a region of previous uniform distribution. During this past summer a study was made at the Bermuda Biological Station on the slippery-dick, *Halichoeres bivittatus*. This fish has longitudinal dark and light stripes. Tissue exchanges were made between these stripes. When made from light to dark the melanophores invaded the transplanted tissue. In the reverse transplants, the melanophores degenerated. In scales regenerating in the dark stripe, cells first appeared at the anterior and posterior edges and later invaded central regions. Experiments were tried under various light conditions, such as in dark aquaria, in diffuse light, bright sunlight with light background, and with dark background. The chromatophores invaded the white transplanted tissue least rapidly in the dark and more rapidly in the order named above, with the fastest rate in fish kept in the sunlight on a dark background. In transplants from dark to light the cells usually disintegrated at the same rate under all conditions. There appeared to be a reservoir of melanoblasts in the dark stripe which is absent in the white stripe.

## Bibliography.


Goodrich, H. B. and Anderson, Priscilla L. Variations of color pattern in hybrids of the goldfish, *Carassius auratus*. *Biol. Bull.*, 77(2):184-191, 1939.

Goodrich, H. B. and Nichols, Rowena. Scale transplantation in the goldfish, *Carassius auratus*. I. Effects on chromatophores. *Biol. Bull.*, 65(2):253-259, 1933.

Goodrich, H. B. and Trinkhaus, J. P. The differential effect of radiations on mendelian phenotypes of the goldfish, *Carassius auratus*. *Biol. Bull.*, 77(2):192-199, 1939.

Lopashov, G. V. *C. R. (Doklady) Acad. Sci., U. S. S. R.*, 44:169, 1944.

Oppenheimer, Jane M. Potencies for differentiation in the teleostean germring. *Jour. Exp. Zool.*, 79(2):185-212, 1938.

Stockard, Charles R. The origin of blood and vascular endothelium in embryos without a circulation of the blood and in the normal embryo. *Amer. Jour. Anat.*, 18(2):227-327, 1915.

———— A study of wandering mesenchymal cells on the living yolk-sac and their developmental products: chromatophores, vascular endothelium and blood cells. *Amer. Jour. Anat.*, 18(3):525-594, 1915.


Discussion by Priscilla Rasquin, American Museum of Natural History, New York.

It would be interesting to know whether the transplanted white scales would acquire melanophores if the host fish were kept in total darkness. It has been shown (1) that certain blind cave fishes *(Anoptichthys hubbsi)* acquire melanophores after some months of living in the light, not only in the dermis and in the meninges but also in the peritoneum. No such peritoneal chromatophores have been noted in this species,

either when they are kept in darkness in the laboratory or when examined in the condition in which they are found in the total darkness of their natural habitat. It is difficult to see how these cells could have appeared in the peritoneum by a migration process, and they certainly have not appeared by an infective process such as Dr. Medawar has described, for they are completely isolated cells. Dr. Goodrich's idea of a "reservoir" of chromatoblasts in the fish dermis may also apply to the perineural and coelomic pigmentation. It is also interesting to note that the appearance of melanophores in these blind fish kept in the light is not mediated optically in any way. The fish lack a lens and retina, and many specimens also lack an optic nerve.

Reference.

1. Rasquin, P. Progressive pigmentary regression in fishes associated with cave environments. *Zoologica*, 32(4):35-42, 1947.

## The Origin of Modifying Genes that Influence the Normal and Atypical Growth of Pigment Cells in Fishes.*

Myron Gordon.

*New York Aquarium, New York Zoological Society.*

In natural populations of platyfishes and swordtails no melanotic tumors were discovered in more than 10,000 specimens. Under laboratory conditions, when a spotted member of one natural population is mated to that of another, tumors develop in their spotted hybrids.

When a platyfish, *Platypoecilus maculatus*, with the spotted (macromelanophore) pattern is mated with the related genus, the swordtail, *Xiphophorus hellerii* (with which it is sympatric in southern Mexican rivers), the spotted intergeneric hybrids develop melanomas. When the spotted *Platypoecilus maculatus* is mated with another platyfish species (whose natural habitat is a thousand miles to the north), *Platypoecilus couchianus*, from the Rio Grande, the spotted interspecific hybrids also develop melanomas. When a spotted *Platypoecilus maculatus* is mated to a member of a nearby species, *Platypoecilus variatus*, from the Rio Panuco, the degree of atypical pigment cell growth in the spotted hybrids is less severe.

When a spotted *Platypoecilus maculatus* from the Rio Coatzacoalcos is mated to a member of the *same* species, *Platypoecilus maculatus*, from the Rio Jamapa, the *intraspecific* spotted hybrids show a definite melanosis very much like those between *P. maculatus* and *P. variatus*. The significant point is that the parents in each type of mating (intergeneric, interspecific, intraspecific) represent *different genetic populations*. Melanomas or melanoses develop in hybrids in response to a genic imbalance between the genes for macromelanophores, five of which have been identified, and their growth regulators, specific macromelanophore modifying genes, two of which are known.

These results may be explained by the same genetic principles that apply in explaining the origin of organic diversity and the mechanisms of the origin of species. When a population of individuals belonging to a single species is separated into two aggregations, as by a geological accident or by other forces, and that separation is maintained rigidly so that interbreeding between them is prevented, the two populations will, in time, become genetically distinct. The isolated populations become different owing to the ever-occurring, mutational changes. The genic changes that appear in members of the first population are not likely to be the same as the mutations that occur in the second. In time the random mutations accumulate in each of the two populations and eventually they make the two groups recognizably different. The rapidity of the genic changes depends on the size of the breeding population, the environment, as well as upon time. As genetically interpreted, the piling up of these small changes, each meeting the challenge of natural selection successfully, constitutes the very beginning of the speciation process.

There are six known natural populations of the platyfish, *Platypoecilus maculatus*, in the Atlantic coast rivers of Mexico, Guatemala and British Honduras. Each of these six populations differs genetically in the frequencies of five macromelanophore pattern genes. Although these populations have been isolated geographically for more than 300,000 years, their morphological differences are insufficient to indicate an evolutionary change at the subspecific level. They are, however, genetically distinct and these genetic differences can account for the genetic imbalance in the hybrid offspring of members representing different river populations.

Far back in geological time all platyfishes were probably like most fishes of their kind that are uniformly colored, unmarked by macromelanophores. In time the first "spotted" mutant appeared in a platyfish population, and transformed some previously existing cells into *macromelanophores*. The nature of the mutation process is not yet

* Aided by a grant from the National Cancer Institute of the United States Public Health Service.

clear, but it is believed that mutations act like enzymes and affect the body chemically. Like most mutations, the macromelanophore mutation was probably harmful and most likely lethal, because most mutations upset an organism's established genetic balance and this, in turn, upsets the biochemical processes in the developing organism.

Prior to the spotted mutation's successful establishment in the platyfish population, mutations which were to serve, in part, as modifiers and controllers of the activity of macromelanophores must have accumulated first, and then neutralized the lethal effects of the spotted mutants when they reoccurred. The platyfish had to be made ready genetically for the coming of the spotted mutations by first accumulating macromelanophore controlling genes. When ready, the platyfish "accepted" macromelanophores without danger to themselves. However, when a genetically balanced spotted platyfish from the Rio Coatzacoalcos is mated with another normal member from the Rio Jamapa, the new recombination of genetic modifiers of macromelanophore growth is not in balance in the spotted hybrids, and these large pigment cells grow atypically. The hereditary effects of macromelanophores can be demonstrated genetically, as well as the effects of gene modifiers which influence macromelanophore growth patterns. The macromelanophores are genetically labile cells subject to normal or typical growth by a series of modifying genes.

REFERENCES.

DOBZHANSKY, TH. Genetics and origin of species. Columbia Univ. Press, 1941.

GORDON, MYRON. Biology of Melanomas. *N. Y. Acad. Sci., Spec. Pub.*, 4:216-268, 1948.

——— *Animal Kingdom*, 52:118, 1949.

——— *Endeavour*, 9:26-34, 1950.

Discussion by W. E. HESTON, National Cancer Institute, Bethesda, Md.

The observations of Dr. Gordon are of especial interest to one studying the inheritance of cancer in mice because of the parallels to his observations that have occurred with mice. In general one can expect a greater variety of tumors to occur in hybrids between two inbred strains of mice than occur in either inbred strain. Little reported that in the $F_1$ hybrids resulting from crossing *Mus bactrianus* with strain $C_{57}$ black *(Mus musculus)* the incidence of non-epithelial tumors was 39.7%, whereas that for the $C_{57}$ black mice was 13.2% and no such tumors were recorded for the *Mus bactrianus* stock. In the history our experimental colony, 10 mice with tumors of the Harderian gland have occurred, and all of these have been hybrids from a specific cross (strain $C_3H \times$ strain $C_{57}$ black). While this is a rare tumor, its occurrence in these specific hybrids and not in either parent strain or any of the other strains of the colony is remarkable.

The variation in degree of atypical pigment cell growth from melanosis to true melanomas effected by the genotypes of the different types of hybrid platyfish might also be compared with the variation in degree of expression of different genotypes affecting tumor formation in the mouse. This is particularly well illustrated with induced lung tumors. One observes from few to many nodules per animal, depending upon its genotype. Dr. Gordon's observation of melanosis in certain types of hybrids compared with true melanomas in other types suggests that with the carcinogen 5, 9, 10—trimethyl—1, 2—benzanthracene that produces pigmented foci in the skin of mice of certain strains, one might be able to produce true melanomas in other strains or hybrid types with a more suitable genotype.

## *Third Session: Physiological.*

### Introduction.

H. W. CHALKLEY.

*National Cancer Institute, Bethesda, Md.*

The papers in this group hold a place of basic interest. We have had the abnormal pigment cell and its destructive effect on the organism discussed from the pragmatic empirical medical approach. We have had the genetic control of the cell within the organism discussed. Now we turn to the normal cell and its biologic behavior, considered as acting as an individual entity functioning cooperatively with other cells within the organism, its growth differentiation and regeneration, and the part it plays as a normal component of the organism.

It is this behavior that in the end will serve as a criterion for all theories of its structure or of the physical and chemical mechanisms posited as inherent in the cell. This is how it behaves as a biological entity and it is this behavior that we are seeking to understand by the biochemical or biophysical approach. Its abnormal behavior, as for instance in cancer, will eventually also be comprehended as a part of this story.

## Pigment Spread in Guinea Pigs.

P. B. MEDAWAR.
*University of Birmingham, England.*

It has been known for more than fifty years that the pigmentation of the superficial epidermis creeps from the colored into the white areas of recessively spotted guinea pigs, whether from grafts or, during normal life, across natural color boundaries. Analysis of the phenomenon has led to the suggestion that "pigment spread" is due to a permanent and serially propagable transformation of the dopa-negative, non-pigmentary dendritic cells of white skin areas into the pigmentary dendritic cells (epidermal melanophores or melanoblasts) characteristic of colored areas. According to this hypothesis, pigment spread is made possible, anatomically, by the fact that dendritic cells form a partially syncytial web throughout the basal layer of the epidermis, whatever its color pattern, and whether it is pigmented or not; and physiologically, by the fact that the epidermal dendritic cell is "cytocrine" in activity (Masson's term) and can presumably "infect" neighboring dendritic cells through a cytoplasmic anastomosis much as (in a trivial sense) it "infects" the Malpighian cells of the epidermis with melanin granules.

It is a shortcoming of this hypothesis that the non-pigmentary dendritic cells (leucophores or "white melanophores") of the colorless areas of spotted guinea pigs, on whose existence the truth of the hypothesis clearly depends, have not yet been seen in living skin. They are revealed by impregnation with acid gold chloride. This shortcoming is to some extent remedied by the fact that black pigmentation will encroach upon the *red* areas of spotted red-black or tricolor guinea pigs, though much more slowly than upon white. Red melanophores are visible in the living epidermis and are present in the same number and distribution as are black melanophores in black skin. Red skin transformed by pigment spread into black contains black melanophores only: either the red melanophores have been converted into black melanophores, or they have been by some unknown mechanism individually replaced and destroyed by them.

Epidermal epithelia lacking dendritic cells are non-infectable.

Pigmentation may be propagated from a black skin area of one guinea pig to a white skin area of another guinea pig if a minute quantity of a suspension in Ringer's solution of the basal layer cells of the black epidermis is "grafted" in such a way as to give the donor melanophores direct access to the "white" melanophores of the recipient. So initiated, foreign pigmentation has been observed to spread over an area as great as 500 mm$^2$, and in certain proportion of cases appears to survive indefinitely. But foreign pigmentation of any area or time of standing may be bleached out at will by transplanting skin from the donor animal whose cells started the foreign pigmentation to the recipient in which it is spreading. This response is thought to be the consequence of an active immunization, and it is believed that foreign pigmentation, though certainly *initiated* by living foreign cells, is maintained and propagated by the multiplication within host cells of some antigenically foreign cytoplasmic ingredient.

"Infective" behavior by constituents of the cytoplasm cannot but be a phenomenon of the greatest rarity: if the authors' interpretation is correct, it is made possible in the present instance by the cytocrine activity of dendritic cells, their semi-syncytial layout, and the co-existence of dendritic cells of different pigmentary activity in a single spotted guinea pig.

### REFERENCES.

BILLINGHAM, R. E. and MEDAWAR, P. B. Pigment spread and cell heredity in guinea pigs' skin. *Heredity*, 2:29-47, 1948.

——— "Infective" transformations of cells. *Brit. J. Cancer*, 2:126-131, 1948.

——— Pigment spread in mammalian skin: Serial propagation and immunity reactions. *Heredity* (in the press), 1950.

### Discussion by MORRIS FOSTER, Columbia University, New York

If the semi-syncytial network provides the path by means of which infectively transforming cytoplasmic particles pass from black-pigment-producing dendritic cells into "white" or into red-pigment-producing cells, and if the same type of transmission mechanism is responsible for "inoculating" Malpighian cells with melanin granules, then some infectively transforming particles should pass into the Malpighian cells along with the melanin granules, thereby infectively transforming the Malpighian cells as well. Since, however, Malpighian cells are not induced to form melanin, it is necessary to make subsidiary hypotheses. For example, one could assume that the cytoplasm in the Malpighian cell contains substances hostile to the action of the infectively transforming particles passing into it from the dendritic cell. If this be the case, however, then the cytoplasmic flow must always be in one direction only, into the Malpighian cell, since a reverse flow would inhibit pigment production in the dendritic cell.

### Discussion by ERNST CASPARI, Wesleyan University, Middletown, Conn.

I was most interested to learn that the spreading phenomenon also occurs at the border of black and red areas, since this situation might well provide critical evidence for the theory of transmission of pigment precursors. Under this theory it would be expected that cells containing both red and black granules would exist in the border region. I wonder particularly whether it would be possible to observe this phenomenon di-

rectly in tissue cultures of black and red melanophores.

**Reply by Medawar.**

The question of whether "infected" red melanophores contain both red and black pigmentary systems, or black alone, is certainly of first-rate importance. Although we are not very optimistic about the use of tissue culture, we hope that really detailed histological analysis will help to solve the problem.

## Atypical Pigment Cell Differentiation in Embryonic Teleostean Grafts and Isolates.

JANE M. OPPENHEIMER.

*Department of Biology, Bryn Mawr College, and Osborn Zoological Laboratory, Yale University, New Haven, Conn.*

The occasional development of red blood corpuscles and of chromatophores is a condition which sometimes obtains in otherwise nondifferentiating isolates and grafts from young teleostean embryos (Oppenheimer, 1949). Examples of such atypical differentiation have occurred in three separate series of experiments (Oppenheimer, 1936a, 1938) to be discussed below.

*Fundulus germ-ring grafts.* In this series of experiments, portions of the germ-ring located 90° or 180° from the midline of the embryonic shield of *Fundulus heteroclitus* gastrulae (cf. fig. 1B, Oppenheimer, 1938) were grafted to the embryonic shield or to the extra-embryonic membrane of gastrulae of the same species. In 37 cases either the whole grafts or portions of them continued development but failed to undergo typical histogenesis and differentiated no axial structures. In 16 of these, however, red blood corpuscles differentiated, and in 10 of these 16 grafts melanophores differentiated. In some cases, only a single melanophore was differentiated within the grafts, in others a larger number was present. Only those grafts are included among the 10 positive cases which contained melanophores located more or less centrally in the mass of cells; grafts to which melanophores were applied only at the surface are excluded from consideration in the possibility that in these cases host melanophores might have migrated to cover the grafts.

Only heteroplastic transplantation or the grafting of materials from vitally stained embryos can furnish direct proof that the melanophores are formed by graft rather than host cells in such experiments as these. Fortunately, however, supplementary data are available from other types of experiment which demonstrate that chromatophores are also similarly differentiated in some cases by isolates rather than transplants from young teleostean embryos.

*Epiplatys germ-ring isolates.* The embryos of *Epiplatys fasciolatus* can be divided at late gastrula stages in such a way (cf. fig. 1A, Oppenheimer, 1938) that the portion of the germ-ring most remote from the embryonic shield can be isolated with part of the yolk from the portion of the egg containing the shield. Such isolates develop for several days in Ringer's solution. Though in some cases they exhibit certain phenomena of growth which simulate the form of the tail, they undergo no histogenesis of axial structures. Of 12 such aggregates studied, one developed red blood corpuscles, one formed a single melanophore and a third differentiated a number of xanthophores. One explant of prospective tailbud region, isolated immediately after the closure of the blastopore, formed both melanophores and xanthophores although otherwise undifferentiated.

*Fundulus isolated blastoderms.* Blastoderms of *Fundulus heteroclitus* separated from the yolk during cleavage stages and cultivated in double-strength Holtfreter's solution under some conditions form hyperblastulae, masses of nondifferentiated cells provided with a large vesicle at one pole (Oppenheimer, 1936a). Of approximately 75 hyperblastulae studied, only one developed a single melanophore of typical size and configuration.

*Discussion and conclusions.* The production of chromatophores by the grafts and isolates described above suggests that in the teleosts under certain experimental conditions pigment cells can be differentiated by cells which normally do not contribute to the teleostean counterpart of the neural crest. The 90° germ-ring of *Fundulus* normally contributes primarily mesoderm to the embryo (Oppenheimer, 1936b); and the 180° germ-ring is unrelated to nervous system formation except insofar as it contributes to the tailbud blastema from which neural derivatives may later arise. While it is theoretically possible, it is highly improbable that the chromatophores in these cases have been differentiated only by the particular cells destined to form them later after their passage through the tailbud blastema. The differentiation of pigment cells under these conditions is therefore presumably the result of what the experimental embryologists call *bedeutungsfremde Selbstdifferenzierung*.

This interpretation, however, is not incompatible with the possibility that in teleosts the chromatophores normally arise from cells corresponding to those of the neural crest of other vertebrates, as suggested by the results of the transplantation experiments of Lopashov (1944) on three species of teleosts, and in line with the neural crest

origin of pigment cells in amphibians (DuShane, 1935), birds (Dorris, 1938) and mammals (Rawles, 1947). It merely signifies that under certain abnormal conditions, other than the usual cells can take over the function of pigment cell formation.

BIBLIOGRAPHY.

DORRIS, F. The production of pigment in vitro by chick neural crest. *Arch. Entw.-mech.*, 138: 323-334, 1938.

DUSHANE, G. P. An experimental study of the origin of pigment cells in Amphibia. *J. Exp. Zool.*, 72: 1-31, 1935.

LOPASHOV, G. V. Origin of pigment cells and visceral cartilage in teleosts. *C. R. (Doklady) Acad. Sci. U. S. S. R.*, 44: 169-172, 1944.

OPPENHEIMER, J. M. The development of isolated blastoderms of Fundulus heteroclitus. *J. Exp. Zool.*, 72: 247-269, 1936 (a).

———— Processes of localization in developing Fundulus. *J. Exp. Zool.*, 73: 405-444, 1936 (b).

———— Potencies for differentiation in the teleostean germ-ring. *J. Exp. Zool.*, 79: 185-212, 1938.

———— Atypical pigment-cell differentiation in embryonic teleostean grafts and isolates. *Proc. Nat. Acad. Sci.*, 35:709-712, 1949.

RAWLES, M. E. Origin of pigment cells from the neural crest in the mouse embryo. *Physiol. Zool.*, 20: 248-266, 1947.

## Regeneration of Neural Retina and Lens from Pigment Cells in the Eyes of Adult Salamanders.*

L. S. STONE.

*Anatomical Laboratory, Yale University School of Medicine, and the Osborn Zoological Laboratory, Yale University, New Haven, Conn.*

The neural retina of adult salamander eyes degenerates when deprived of its blood supply either by severing the vessels which vascularize it (Stone and Chace, 1941) or by transplanting the entire eye (Stone and Zaur, 1940; Stone and Cole, 1943; Stone and Ellison, 1945). The only retinal cells which survive are those of the pigmented epithelial layer from which a new neural retina regenerates (Stone, 1949). This has been studied in detail in many grafted adult urodele eyes. Degeneration spreads throughout the neural retina during the first three weeks. It often proceeds at different rates in various parts of the same eye, allowing early stages of regeneration to begin in some areas while adjacent regions are still degenerating. The true origin of the new neural retina is therefore more easily followed in cases where degeneration is simultaneous in all parts or where the entire neural retina is detached from the underlying retinal pigment layer by a gentle stream of Ringer's solution and then removed intact through a broad dorsal slit in the eye.

Degeneration of the neural retina in grafted eyes usually spreads rapidly until the retinal pigment cells are finally denuded and the cellular debris is absorbed above them. The pigment cells then become dense black oval or flattened bodies resembling those found soon after surgical removal of the entire neural retina. Now they take on temporarily another function, entering the critical stages which can be followed step by step as they determine the origin of the new neural retina.

These pigment cells increase markedly in size. Their nuclei become distinct as they undergo mitosis. One daughter cell migrates inward, loses its pigment and with similar ones forms a sharply defined layer, which by further cell division gives rise to a new neural retina. The other daughter cell retains its pigment and later takes on the status of a retinal pigment cell when the neural retina above it has fully regenerated. The functional capacity of this cell is finally expressed by the migration of its pigment granules in a light-adapted eye as soon as the rods and cones above it are differentiated.

When a small portion of the neural retina is excised, or is detached as a permanent elevated fold, regeneration is also called forth from the underlying retinal pigment cells. On the other hand the initial reaction of the pigment cell to a small retinal injury is one of rapid mitosis and mass migration into the wound, somewhat similar to that found in the retinal wounds of other vertebrates. However, in the urodele retina these cells later lose their pigment and differentiate into neural retinal tissue. Retinal pigment epithelium transplanted into the eye chambers also gives rise to neural retina.

Since the early pigment cell changes involve replacement of a lost tissue the term "dedifferentiation" might be considered as it applies to them. This term is often loosely and obscurely applied to cells which are assumed to be taking part in regeneration, although up to that moment they are recognized as highly differentiated elements with special morphological and functional characteristics. Under the proper stimulus they are supposed to lose their special features and take on a role of supplying new cells that will later develop into similar or different elements. If the term is defined in this sense it can be said that the retinal pigment cell in the salamander eye is capable of dedifferentiation.

Another pigment cell in the eye of *Triturus* salamanders may be considered in the same category, for when the lens is removed the

* Aided by grants from the James Hudson Brown Fund and the United States Public Health Service.

heavily pigmented cells along the free pupillary margin of the dorsal iris increase in size, become depigmented, undergo mitosis and form a vesicle that develops into a lens (Wachs, 1914, and others). When the latter becomes detached the cells in the dorsal iris regain their normal appearance. If varying amounts of dorsal iris are replaced by non-lens regenerating ventral iris, two widely separated lenses develop from the remaining dorsal pupillary margins after removal of the original lens. Secondary pupils experimentally produced in various regions of the dorsal iris by the insertion of pieces of pliofilm or cornea show that potentiality for lens formation is quite widely distributed and not confined to the free pupillary margin (Stone and Vultee, 1949).

These changes in the pigment cells can be experimentally inhibited by the following: 1) the presence of a transplanted normal lens of the same or another species (Stone, 1945); 2) the presence of a thirty-day lens regenerate (Stone, 1943); 3) injections of aqueous humor from eyes containing lenses (Stone and Vultee, 1949); 4) the presence of some carcinogens.

### Literature Cited.

Stone, L. S. Factors controlling lens regeneration from the dorsal iris in adult *Triturus viridescens* eyes. *Proc. Soc. Exp. Biol. and Med.*, v. 54, 102-103, 1943.

———— Heteroplastic lens grafts related to factors inhibiting lens regeneration in *Triturus. Proc. Soc. Exp. Biol. and Med.*, v. 60, 10, 1945.

———— Return of vision and functional polarization in the retinae of transplanted salamander eyes. Exp. Cell Research, Sup. 1, 582-584. (*Proc. 6th Intern. Cong. Exp. Cytol., 1947*), 1949.

Stone, L. S. and Chace, R. R. Experimental studies on the regenerating lens and the eye in adult *Triturus viridescens. Anat. Rec.*, v. 79, 333-348, 1941.

Stone, L. S. and Cole, C. H. Grafted eyes of young and old adult salamanders (*Amblystoma punctatum*) showing return of vision. *Yale J. Biol. and Med.*, v. 15, 735-756, 1943.

Stone, L. S. and Ellison, F. S. Return of vision in eyes exchanged between adult salamanders of different species. *J. Exp. Zool.*, v. 100, 217-227, 1945.

Stone, L. S. and Vultee, J. H. Inhibition and release of lens regeneration in the dorsal iris of *Triturus v. viridescens. Anat. Rec.*, 103, 144-145, 1949.

Stone, L. S. and Zaur, I. S. Reimplantation and transplantation of adult eyes in the salamander (*Triturus viridescens*) with return of vision. *J. Exp. Zool.*, v. 85, 243-269, 1940.

Wachs, H. Neue Versuche Zur Wolff'schen Linsenregeneration. *Arch. f. Entwmech. d. Org.*, Bd. 39, 384-451, 1914.

## X-Ray Effects on Mouse Pigmentation as Related to Melanoblast Distribution.

Herman B. Chase & Virginia W. Smith.
*Department of Biology, Brown University, Providence, R. I.*

Several features of the x-ray-induced greying response suggest certain properties of the pigmentation system. Follicles react largely as independent units, producing fully pigmented hairs (no apparent gross effect), white hairs, or infrequently mosaics. The effect is permanent or toward more white hairs in successive hair generations of the particular follicle (Chase, Quastler, and Skaggs, 1947; Chase, 1949). The percentage of follicles producing only white hairs after treatment increases with dose (200-1000 r) and with dose-rate. The percentage for a given dose is greater for follicles treated in catagen and telogen stages and for follicles of the smaller hair types (Chase, 1949; Chase and Rauch, in press). In a mosaic some of the medullary and cortical cells lack pigment granules entirely, some have a full complement, and some have a reduced number of granules. These various cells are arranged irregularly throughout the length of the hair. With increasing size of hairs (such as awls in the mouse, most of the hairs in rabbits and cats, all of the hairs in guinea pigs), the follicles are less "sensitive" to a given dose of x-radiation, produce a greater frequency of mosaics, and display less difference in response when treated in telogen or in anagen phases. It would seem that susceptible elements must be few in number, very few in smaller follicles. At beginning of anagen there would be a moderate increase of these elements but little, if any, further increase during the anagen phase (2 to 17 days post-plucking). After the initial supply for the original follicle invagination, there would be no new invasion for subsequent hair generations.

Following Masson's (1948) definitions the dendritic cells which eventually produce pigment are termed melanoblasts whereas the recipient cells, if any, are termed melanophores. Melanoblasts generally are not observed because of their fragility with certain standard histological methods and because they are largely obscured after the matrix cells become pigmented. Phase microscopy with the Spencer B minus contrast low, oil immersion objective on unstained frozen sections has proved most revealing. In young mice, melanoblasts of the basal layer of the skin epidermis can be seen to be incorporated in the original invaginations of newly-forming follicles. In early anagen stages of subsequent hair generations, melanoblasts are found in the permanent external sheath (continuous with basal layer of skin epidermis) or in the derivative basal layer of the bulb. They become melanogenic with fine dispersed granules and send long dendritic processes to the matrix cells. Later, beginning about 6 days post-plucking, the "inoc-

ulated" matrix cells (= melanophores) exhibit characteristic dense pigmentation. The keratinized hair shaft arises from these matrix cells. Pigmented matrix cells seldom divide, but new cells arise from the proliferating lower bulb and receive pigment as they pass by the melanoblast processes of the upper bulb. As few as 4 melanoblasts have been observed to supply the stream of matrix cells of a small follicle (zigzag) and the presence of only one or two results in a mosaic.

From histological and x-radiation evidence it appears that the "reservoir" of melanoblasts is within the epidermal follicle (cf. Taylor, 1949). Dermal melanophores apparently do not contribute to pigmentation in the hair follicle. The epidermal melanoblasts are the original granule-forming cells, but in the recipient matrix cells, the characteristic shape and color of the phenotype are further imposed upon the granules. Whereas biotin deficiency, for instance, causes a failure of melanin-formation on these granule sites (Chase and Rauch, in press), x-radiation destroys the source of supply of granules, namely, the epidermal melanoblasts of the follicle.

(Work supported by grant-in-aid from American Cancer Society, recommended by Committee on Growth of National Research Council).

REFERENCES.

CHASE, H. B. Greying of hair. I. Effects produced by single doses of x-rays on mice. *J. Morph.*, 84: 57-80, 1949.

CHASE, H. B., H. QUASTLER AND L. S. SKAGGS. Biological evaluation of 20 million volt roentgen rays. II. Decoloration of hair in mice. *Am. J. Roent. and Rad. Ther.*, 57: 359-361, 1947.

CHASE, H. B. AND H. RAUCH. Greying of hair. II. Response of individual hairs in mice to variations in x-radiation. In press.

MASSON, P. Pigment cells in man. *Spec. Publ. N. Y. Acad. Sci.*, 4: 15-37, 1948.

TAYLOR, A. C. Survival of rat skin and changes in hair pigmentation following freezing. *J. Exp. Zool.*, 110: 77-111, 1949.

## A Comparative Colorimetric Study of Dopa-melanin Formation by Melanomas and Pigmented Skins.

RUTH E. SHRADER & CARROLL A. PFEIFFER.

*Department of Anatomy, Yale University School of Medicine, New Haven, Conn.*

The costo-vertebral pigmented skin spot of the Syrian hamster, which contains both intradermal dentritic pigmented cells and exceptionally large pigmented hair roots[1] has proved to be consistently dopa-negative in histological sections prepared according to several standard technical procedures[2,3]. A method utilizing photo-electric colorimetric evaluation of dopa-melanin has been evolved which permits comparison of this pigmented tissue with other tissues which can be shown by histological means to be dopa-positive.

Skin specimens were surgically removed, freed of hair and unpigmented skin, chilled to 4° C., minced in a few drops of phosphate buffer, and rapidly weighed on small squares of clean coverslip using a microtorsion balance. Increasing weights of minced tissues were placed in centrifuge tubes containing 2 ml. of freshly prepared 1:1000 1-dopa solution, buffered to pH 7.4, and thoroughly mixed. After four hours' incubation at 37° C. the tubes were centrifuged at 25,000 rpm. for 15 minutes. The supernatant fluid was decanted, diluted to a standard volume, and kept in chilled colorimeter tubes until read on a Klett-Summerson photo-electric colorimeter using a KS-42 filter. The auto-oxidative rate of dopa was determined for each experiment by means of a control tube containing only buffered dopa. The control tube was given a value of 100% and the values obtained for the different tissue samples were compared with it.

Using this technique, experiments were done on tissues from the Cloudman mouse melanoma and from human melanomas. These tumor tissues gave almost straight line curves with the activity (color formation) increasing directly with the weight of the tissue samples. The results agree favorably with those obtained from Warburg studies of the enzyme activity of such melanoma tissues[4].

A number of types of skin were studied by this method. These included skin from the neck, flank and pigment spot of the hamster, pigmented nipples from guinea pigs, neck and flank skin from mice, adult and infant human skin, including depigmented and hyper-pigmented negro skin. In contrast to the straight line activity curve of the tumor tissue, these skins showed a biphasic activity curve with the final inclination in the downward direction. This characteristic of pigmented skins has been interpreted to indicate the presence of inhibitory substances which interfere with the formation of dopa-melanin. This observation is in agreement with previous work showing such inhibitory substances to be present in the skins of guinea pigs[5], rabbits[6,7] and man[8,9].

When the conditions of the experiment were changed so that the weight of the tissue was held constant and the concentration, but not the volume, of the dopa solution was increased, a curve was obtained which is suggestive of the classic "substrate competition" curve. The addition of a sulfhydril substance, glutathione[10] increased the inhibition of color formation in dilute dopa solutions but did not significantly affect higher concentrations.

The effect of hormonal stimulation of pigmentation upon the ability of the stimulated skin to form dopa-melanin was investigated, using both the pigmented nipple of the guinea pig and the hamster pigment spot. In both instances, tissues which had been caused to hypertrophy and blacken under hormonal influence gave increased color formation with dopa as contrasted with untreated control tissues, but the essential biphasic shape of the curves was unchanged.

### References.

1. Shrader, R. E. Development of the dimorphic pigment spot of the Syrian hamster. *Anat. Rec.*, 105:561, 1949.
2. Laidlaw, G. F. The dopa reaction in normal histological technic. *Anat. Rec.*, 53:399, 1932.
3. Becker, S. W. Cutaneous melanoblasts as studied by the paraffin dopa technic. *J. Invest. Derm.*, 5:463, 1942.
4. Greenstein, J. P. and Algire, G. H. Comparative oxidase activity of melanotic ÷ amelanotic melanomas. *J. Nat. Can. Inst.*, 5:35, 1944.
5. Schaaf, F. Manometrische Vergleichsuntersuchungen mit Presssäften aus Weisser und Pigmentierter Meerschweinchenhaut. *Arch. f. Dermatol., u. Syph.*, 176:646, 1938.
6. Pugh, C. E. M. Tyrosinase from the skin of certain black rabbits. *Bioch. J.*, 27:475, 1933.
7. Koller, P. On pigment formation in the D-black rabbit. *J. of Genetics*, 22:103, 1930.
8. Rothman, S., Krysa, H. F. and Smiljanic, A. M. Inhibitory action of human epidermis on melanin formation. *Proc. Soc. Exp. Biol. and Med.*, 62:208, 1946.
9. Flesch, P. Inhibitory action of extracts of mammalian skin on pigment formation. *Proc. Soc.. Exp. Biol. and Med.*, 70:136, 1949.

**Discussion by Morris Foster, Columbia University, New York.**

Two important sources of error are inherent in the techniques used: (1) The colorimetric method, whereby pigment production rate is equated with oxidase activity. Such reasoning could be erroneous. For example, a reducing agent reacting with a substance produced after the oxidation of dopa could inhibit pigment production without affecting dopa oxidase activity; although, on the basis of colorimetric criteria, inhibition or lack of enzyme activity would be inferred. (2) The use of dopa as a substrate, since dopa can be oxidized via both the phenolase and cytochrome systems, whereas tyrosine is not affected by the latter. Thus enzymatic oxidation of dopa could be wholly or partly attributed to the cytochrome system rather than to the phenolase system. (See paper by Hesselback et al.)

A more direct measure of phenolase activity could be obtained by using tyrosine as the substrate and by measuring the rate of oxygen consumption in a Warburg respirometer.

In regard to the hamster pigment spot, an explanation of increasingly inhibited oxidative activity with increasing weight of pigment spot sample is difficult to make, since larger samples should also give larger amounts of enzyme, resulting in increased rather than decreased activity.

**Reply by Shrader & Pfeiffer.**

We would like to strongly emphazise that we do not know the enzyme system or systems involved in the production of dopa-melanin in these experiments. Our experiments were not designed primarily to elucidate the mechanisms of melanin formation but were intended to explain why the dopa reaction could not be obtained on sectioned hamster pigment spot. What we measured was the amount of dopa-melanin that was produced under experimental conditions as similar as possible to those of histological methods. The use of tyrosine as a substrate, or the Warburg apparatus as a method, would not have served to answer our original question. We do, however, feel that the results obtained justify the assumption that the colorimetric measurement of dopa-melanin is a valid criteria for an estimation of the pigment forming ability of the tissue.

In regard to the increase in inhibition which occurs as hamster pigment spot tissue weight is increased, we can only say that this is a characteristic of all skins tested and that we have postulated that it represents the results of some type of competitive action between the enzyme and inhibitor systems for utilization of the substrate. This suggested explanation gains further support from the fact that such inhibition is more marked when the quantity of available substrate is low and can be overcome by the addition of more substrate.

## *Fourth Session: Biochemical and Biophysical.*

### Introduction.

Jesse P. Greenstein.
*National Cancer Institute, Bethesda, Md.*

Melanin chemistry may be roughly divided into two general approaches: (a) the character of the pigment noted in natural sources, i.e., the intracellular granules in skin, hair, plants, etc., and (b) the nature of the polymeric pigments obtained by the *in vitro* oxidation of such amino acids as tyrosine and dihydroxyphenylalanine, and the relation, if not the identity, of such pigments to those noted in natural sources. As yet, no clearcut

evidence has linked the synthetic pigments under (b) with the pigments derived from natural sources, although the presence of dopa oxidase in melanin-containing melanoblasts, and the absence of this enzyme from amelanotic tissues are more than suggestive of a connection between the two.

The natural pigment is generally associated with protein in the form of cytoplasmic granules. These granules themselves contain dopa oxidase activity, and an essential problem which requires clarification is whether the pigment may be preformed from small molecular weight precursors followed by conjugation with one or more proteins in the cytoplasmic complex or whether it is derived from certain potentially chromophoric groups (tyrosine residues) existing at the surface of the protein molecules of the complex. It is a matter of some difficulty to free the pigment completely of protein, and even when this is accomplished the vigorous methods required raise some doubt as to whether the melanin has not been altered to some extent. Indeed, the characterization of the particulate, sub-unit components of any cell, and the separation of the various members of these particulate components, demand techniques which for the most part are not yet adequately developed. However, advances in this, as in other fields, may come from many able quarters. That such advances have been made in several approaches to the problem of pigment chemistry are shown in the excellent papers which follow.

## Mammalian Melanin Formation: I. Biochemical Studies.

A. Bunsen Lerner,
*University Hospital, University of Michigan, Ann Arbor, Mich.*
&
Thomas B. Fitzpatrick,
*Fellow in Dermatology and Syphilology, Mayo Foundation, Rochester, Minn.*

Investigation of the biochemistry of melanin formation in plants, insects and marine animals had shown that the enzyme, tyrosinase, catalyzes the oxidation of L-tyrosine to dihydroxyphenyl-L-alanine (dopa), and then the oxidation of dopa to melanin. Until recently, however, the presence of tyrosinase in mammalian tissue had not been demonstrated conclusively, and it was believed that melanin in mammalian tissue is formed by a mechanism different from that operating in other species. Histochemical evidence indicated that mammalian skin contains an enzyme, "dopa oxidase," which catalyses the oxidation of dopa, but not tyrosine, to melanin. Largely as a result of these beliefs, two separate hypotheses of melanogenesis evolved: 1) melanin formation in insects and plants was associated with tyrosinase, while 2) melanin production in mammalian skin was associated with dopa oxidase. Recent evidence has shown that these separate concepts can now be merged into a single hypothesis to account for melanin formation in man, lower animals, insects and plants (1). It is now known that the original distinction between tyrosinase and dopa oxidase is no longer valid. Hence, it is suggested that the single term, tyrosinase, should be used instead of the separate terms, tyrosinase and dopa oxidase (2).

While tyrosinase obtained from different species has some unique properties, depending on the particular source, three characteristics are common to tyrosinase, under proper conditions, regardless of its origin: 1) all catalyze the oxidation of tyrosine to melanin, 2) the enzymatic reaction with the monohydroxyphenyl compound is catalyzed by some orthodihydroxyphenyl compound (dopa, catechol, etc.), and 3) copper is associated with the activity of the enzyme.

When tyrosine and tyrosinase are allowed to react in the presence of oxygen, there is often a lag period before oxidation of tyrosine begins. This lag interval is referred to as the "induction period." Small amounts of dopa are very effective in shortening the induction period in the tyrosine-tyrosinase reaction. For mammalian tyrosinase there is a linear relationship between the negative logarithm of the dopa concentration and the induction period. Compounds related structurally to dopa, such as epinephrine, catechol and the like can shorten the induction period, but not nearly so effectively as dopa does. When dopa itself is used as a substitute for tyrosine, there is no induction period.

Dopa participates in the tyrosine-tyrosinase reaction in at least three ways: 1) dopa is formed from tyrosine, 2) dopa catalyses the tyrosine-tyrosinase reaction, and 3) some amount of dopa is reformed during the conversion of dopa to melanin.

Various substances inhibit melanin formation *in vitro* and *in vivo*. The mechanism of inhibition is dependent upon the particular step in the tyrosinase-catalyzed series of reactions in which the conversion of tyrosine to dopa and eventually to melanin is blocked.

### References.

1. Lerner, A. B. and Fitzpatrick, T. B. Biochemistry of Melanin Formation, *Physiol. Rev.*, 30:91-126, Jan., 1950.
2. Lerner, A. B., Fitzpatrick, T. B., Calkins, Evan and Summerson, W. H. Mammalian Tyrosinase: Preparation and Properties. *J. Biol. Chem.*, 178:185-195 (Mar.), 1949.

## Mammalian Melanin Formation: II. Histochemical Studies.

THOMAS B. FITZPATRICK,
*Fellow in Dermatology and Syphilology, Mayo Foundation, Rochester, Minn.*
&
A. BUNSEN LERNER,
*University Hospital, University of Michigan, Ann Arbor, Mich.*

As early as 1901 von Fürth advanced the hypothesis that melanin formation is the result of the action of an intracellular oxidase on aromatic or chromogen groups in certain protein molecules. Bloch, a Swiss dermatologist, stimulated by this hypothesis, attempted to prove it by experimental methods. He selected the naturally occurring amino acid, dihydroxyphenyl-L-alanine (dopa), as the substrate for his histochemical studies.

Bloch immersed frozen-fixed sections of human skin in a 1:1,000 solution of dopa buffered to pH 7.3, and noted that after twenty-four hours at room temperature black (melanin) granules were deposited in the cytoplasm of cells located in the basal layer of the epidermis. These specialized cells, which he called " melanoblasts," are located at the epidermal-dermal junction, and were considered by Bloch to be the site of melanin formation. Further evidence was provided by Bloch and his co-workers to support the hypothesis that the melanoblasts contained an enzyme, dopa oxidase, which catalyzed the oxidation of dopa to melanin within the cell. The dopa oxidase hypothesis of human melanin formation as advanced by Bloch never has been generally accepted as the explanation for the chemical mechanism underlying melanin formation. The main criticism has been that dopa never has been demonstrated in mammalian tissue.

In the past eight years it has been firmly established that extracts from mouse, horse and human melanomas contain tyrosinase and dopa oxidase activities (1). Furthermore, it has been shown that under certain conditions no true distinction can be made between tyrosinase and dopa oxidase activities in mammalian tissue. At the time Bloch carried out his important histochemical studies, little was known about the optimal conditions for the enzymatic oxidation of tyrosine. This may account for the fact that Bloch, working with mammalian tissue slices, obtained melanin formation from dopa but not from tyrosine.

In some recent histochemical experiments the authors, in collaboration with S. William Becker, Jr., demonstrated the formation of melanin from tyrosine in human white skin which had been irradiated with ultraviolet radiant energy for seven days before excision. Tissue slices cut from the biopsy material were incubated in tyrosine solutions at pH 7.1 for twenty-four to forty-eight hours. In paraffin sections of this material, there were seen large dendritic melanoblasts containing melanin granules in their cytoplasm, identical in their morphology to the "dopa-positive" cells obtained by Bloch. The catalytic effect of these cells on the oxidation of tyrosine to melanin is absent when the tissue slices are heated for ten minutes at 100°C. or when the tissue slices are incubated with sodium diethyldithiocarbamate, a copper-binding compound, for 6 hours prior to incubation in tyrosine. Since tyrosine, in contrast to dopa, which readily auto-oxidizes, is a stable amino acid which does not oxidize spontaneously to melanin *in vitro*, it is likely that the melanoblasts of human skin contain an intracellular oxidase, *tyrosinase*, similar to the enzyme described previously. The enzyme apparently exists in human skin in a partially inhibited state, and can be activated by ultraviolet radiant energy. The mechanism of this activation is not fully understood, but the inactivation of epidermal sulfhydryl by the ionizing radiation appears to play an important part. The data offer strong evidence that the pigment precursor in human melanin formation is tyrosine and not dopa.

The elaboration of melanin pigment in the epidermal melanoblast ordinarily depends on the available concentration of three substances:

1) The enzyme *tyrosinase:* a copper-protein complex attached to particles in the cytoplasm of the melanoblast.
2) A suitable substrate: usually tyrosine or dopa.
3) Molecular oxygen.

If any of these substances is absent, the formation of melanin is impaired.

The reaction of the three basic substances, tyrosinase, substrate and molecular oxygen, is controlled by several physico-chemical factors which determine the rate of melanin formation:

1) A catalytic substance, usually dopa, which can accelerate the tyrosine-tyrosinase reaction.
2) Chemical groups which normally inhibit copper enzymes, for example, sulfhydryl groups, normally found in the epidermis.
3) Physical and chemical factors, such as temperature, hydrogen ion concentration and oxidation-reduction potentials.

The quantity of melanin produced by the cell depends on the overall balance of these different forces.

### REFERENCE.

1. LERNER, A. B. and FITZPATRICK, T. B. Biochemistry of Melanin Formation. *Physiol. Rev.*, 30:91-126, Jan., 1950.

## Observations on the Structure, Derivation and Nature of Melanin.

E. Meirowsky, L. W. Freeman & R. B. Fischer.

*Indiana University School of Medicine, Indianapolis, Ind.*

Developments in enzyme and cellular chemistry have clearly demonstrated that the nucleus is the center of metabolism of nucleoproteins. The most intense production of nucleoprotein appears to take place in the nucleolus, and the material diffuses to, and through, the nuclear membrane into the cytoplasm. As shown by DuBuy and his coworkers, the melanin of the S91 melanoma contains approximately 20% nucleic acids. This would lead to the suspicion that melanin is closely allied to, or identical with, nucleoproteins, especially when the morphological picture is taken into account.

A series of color slides of pertinent cells will be presented, enlarged 540 times, which give a pictorial representation of the following pattern: Melanin first appears in the nucleolus and spreads to the linin framework of the nucleus. It appears in intranuclear vacuoles and finally involves the entire nucleus and the membrane. It leaves the nucleus by way of the chromidial derivatives.

We are of the opinion that this demonstration clearly indicates that the source of melanin formation is within the nuclear material. It appears that the life history of the melanin—as demonstrated—closely parallels that of chromatin and that nucleoprotein is replaced by melanoprotein.

It can be noted from the pictures to be presented that melanized nuclei show a considerable variation in size, by measurement, from $7 \times 7$ micra up to $16 \times 36$ micra. This raises the question as to whether these larger nuclei result from further growth of the melanized chromatin, or from propagation of individual melanin granules.

Their main features, so far observed, include the characteristics of membranes, an inner body showing amitotic division; "X" bodies which could not be identified, which, however, are an apparatus of propagation, connected with the process of budding and of buckling of the membrane. This process leads to buds connected with the mother-body by fine strands or a solid stem. These buds also show the "X" structure and may undergo severance from the mother body; free buds which no longer can be differentiated from melanin granules; and cloudy masses spreading from melanin granules in which new granules make their appearance.

In general, the youngest buds are colorless and show all transitions to deep coloring, just as described by Smith in his cultures of the pigmented epithelium of the eye. We have, on occasion, succeeded in differentially staining the body and the bud by neutral red as a basic dye and light green as an acid dye. The buds have been seen to stain acidophilic with light green. Supravital staining with borax-methylene blue applied to unfixed specimens by Scott's method often shows the young buds to be colorless. These young buds appear to be without a membrane and as they develop, they stain blue and a membrane makes its appearance.

The most striking feature of all of these buds is the presence of the "X" structure. Entirely the same buds with "X" structures are also found, in very great numbers, separated from melanin granules freely in the specimen.

While further work is warranted, in order to understand the foregoing observations in their entirety, we believe that the outstanding features of melanin granules in melanomas and mammalian choroids are compatible with those of a living, dividing, and budding structure derived from living, dividing and budding nuclear material.

References on the Main Investigations of the Relationship: Chromatin and Melanin.

A. Nucleolus and Melanin.

Roessle, R. Der Pigmentierungsvorgang im Melanosarcom. *Ztschr. Krebsforsch.*, 2:291-332, 1904.

"The most remarkable observation is the extrusion of nucleolar material into the cytoplasm and its transformation into melanin."

Meirowsky, E. Die Entstehung des Oberhautpigments aus der Substanz der Kernkoerperchen. *Monatshefte Prakt. Derm.* 43:155-163, 1906.

———— Ueber den Ursprung des Melanotischen Pigments der Haut und des Auges. Publ. W. Klinkhardt, Leipzig, 1908.

"Formation of pigment is preceded by an augmentation of nucleolar material irrespective of the material under observation (skin of man and rabbits after irradiation, embryonic skin, triton larves, pigment of the eye, nevi melanomas). The nucleolar material is transformed into melanin."

Goda, T. Cytoplasmic Inclusions of Amphibian Cells with Special Reference to Melanin Formation. *J. Faculty of Science Imperial University, Tokyo.* Section IV, Zoology, First Part, Vol. II, 51-122, 1928-1931.

"The melanin granules arise from the nucleus by the following process: nucleolar bodies — nucleoliquid drops — melanogranules."

Schultz, O. T. The Formation of Pigment by the Dermal Chromatophores. *J. Med. Res.*, 26 (new series 21): 65-77, 1912.

". . . chromatin is thrown out of the nucleus into the cytoplasm, leading to the formation of a functional chromatin net. The chromatin present in the cytoplasm becomes changed into a material which has the staining reactions of nucleolar substance. Further change leads to the formation of this material into pigment."

"(Pigment) . . . is the product of the specialized physiological activity of the cell by which nuclear derivates are transformed directly into pigment."

B. Melanization of Nuclei, Chromidia and Mitoses.

VON SZILY, A. Ueber die Entstehung des Melanotischen Pigmentes im Auge der Wirbeltierembryonen und im Choroidealsarkomen. *Arch. Mikr. Anat.*, 77: 1-70, 1911.

"The colorless stromata of the melanin of metazoa originate in all cases examined exclusively in the nucleus. Their direct origin from the chromatin of the nucleus and their transformation into the cytoplasm can exactly be followed up. These 'chromidia' change over into melanin under the influence of ferments."

JELIASKOWA PASPALEWA, A. Cytologische Untersuchungen ueber die Entstehung des Melanotischen Pigments. *Ztschr. Wissenschaftl. Zoologie*, 137: 365-402, 1930.

"The observation of a total melanization of chromosomes makes it impossible to contest the origin of melanin from chromatin."

LUDFORD, R. J. Nuclear Activity during Melanosis with Special Reference to Melanin Formation in a Melanotic Sarcoma. *J. Royal Micr. Soc.*, 13-28, 1924.

——— The General and Experimental Cytology of Cancer. *J. Micr. Soc.*, 249-292, Sept. 1925.

"Melanosis occurring during mitosis and following chromatin extrusion, nuclear fragmentation, nuclear budding, karrhyorrhexis, and pycnosis." Ludford believes that the greatest part of the melanin is formed in the cytoplasm under the influence of the Golgi apparatus which is concerned with enzyme formation.

C. Melanization of Intranuclear Vacuoles.

MEIROWSKY, E. Die Entstehung des Oberhautpigments aus der Substanz der Kernkoerperchen. *Montsh. Prakt. Derm.*, 43: 155-163, 1906.

"A cavity is formed in the nucleus with melanin granules at its wall. Through the ruptured wall pigment is extruded into the protoplasm."

LUDFORD, R. J. Nuclear Activity During Melanosis with Special Reference to Melanin Formation in a Melanotic Sarcoma. *J. Roy. Micr. Soc.*, 13-28, 1924.

Summary 8. "Melanin is often formed inside the nucleus, generally in intranuclear vacuoles."

APITZ, K. Ueber die Pigmentbildung in den Zellkernen Melanotischer Geschwueslte. *Virchow Arch.*, 300: 89-112, 1937.

"The nucleus forms the mother substance of melanin." "The origin of the nuclear melanin takes place within vacuoles owing to the retention of physiological secretion product of the nucleus."

D. Biochemistry of Nucleoproteins.

DEROBERTIS, E. D. P., NOWINSKI, W. M. AND SAEZ, F. A. General Cytology. Publ. W. B. Saunders, Philadelphia and London, 1938.

E. Budding Processes in Individual Melanin Granules.

As far as known, no references are available.

## Evidence for the Mitochrondrial Nature and Function of Melanin Granules.

MARK WOODS, HERMAN DUBUY & DEAN BURK.

*National Institutes of Health, Bethesda, Md.*

Melanin occurs in the cytoplasmic granules of the melanoblasts of the Harding-Passey and Cloudman S91 mouse melanomas, and also, of course, in the phagocytes of these tumors. In both tumors, cells occur in which all, or nearly all, of the visible cytoplasmic granules are melanized. Colorless granules of similar size occur in amelanotic or partially amelanotic cells of the S91 tumor and also in the derived Algire partially amelanotic S91A melanoma. Some colorless granules usually occur in the perikaryon of the Harding-Passey melanoblast. The S91A amelanotic melanoma sometimes contains cells in which the cytoplasmic granules are very slightly melanized.

The cytoplasmic granules (melanized and non-melanized) are the only structures which stain with Janus Green B in the absence of nuclear staining by this dye. The granule staining is reversibly dependent upon oxygen tension. No other structures resembling mitochondria are visible in the cells. On alkaline hydrolysis, both melanized and non-melanized granules yield solutions with strong ultraviolet absorption at 2580A, and contain organic phosphorus and pentose. Centrifugally isolated cytoplasmic granules of amelanotic melanoma cells possess enzymic activities characteristic of mitochondria of other origin (e.g., from liver, kidney, heart). Aerobically, these activities include the cytochrome oxidase and succinic oxidase systems. Anaerobically, the cytoplasmic granules possess glycolytic activities also comparable to those of typical mitochondria. Centrifugally isolated melanized granules from both Harding-Passey and S91 melanomas possess not only all of the enzymic activities found in the amelanotic granules, but also dopa oxidase activity. On the basis of the foregoing morphologic, chemical and enzymic data it is concluded that the melanized and non-melanized granules of these mouse melanomas are mitochondria.

Mitochondria are fundamental structures in both animal and plant cells, and in plants it is now well established that they derive from pre-existing mitochondria, possess a complex hereditary system (chondriogenes), and are capable of mutation. In mutant states plant mitochondria display abnormal enzymic activities. Self-duplication of these abnormal mitochondria results in development of neoplasia. Plant mitochondria may be specifically modified by certain viruses that result in neoplasias very similar to those caused by mutant chondriogenes. The behavior of normal, mutant or virus-modified mitochondria may also be affected by specific nuclear genes.

BIBLIOGRAPHY.

1. WOODS, M. W., DUBUY, H. G., BURK, DEAN AND HESSELBACH, M. L. Cytological studies on the nature of the cytoplasmic particulates in the Cloudman S91 mouse melanoma, *J. N. C. Inst.*, 9: 311-323, 1949.
2. DUBUY, H. G., WOODS, M. W., BURK, DEAN AND LACKEY, MARY D. Enzymatic activities of isolated amelanotic and melanotic granules of mouse melanomas and a suggested relationship to mitochondria. *Ibid.*, 9: 325-336, 1949.
3. DUBUY, H. G. AND WOODS, M. W. A possible common mitochondrial origin of the variegational and virus diseases in plants and cancers in animals. In Am. Assoc. Advancement Sc. Res. Conf. on Cancer, pp. 162-169. Lancaster press (1945).
4. WOODS, M. W. AND DUBUY, H. G. Cytoplasmic diseases and cancer. *Science*, 102: 591-593, 1945.

## Oxidative Activities of Mouse Melanomas with Reference to Melanization.

MARIE L. HESSELBACH, MARK WOODS & DEAN BURK.

*National Institutes of Health, Bethesda, Md.*

*Dopa Oxidase.* In the absence of added cytochrome C, Harding-Passey mouse melanoma homogenates oxidized tyrosine, dopa and catechol, with consumption of oxygen gas and formation of dark brown or black coloration. Cloudman S91 melanoma homogenates acted likewise on dopa and catechol. Tyrosine was oxidized either not at all or following a variable lag period. Similarly prepared homogenates of the derived Algire partially amelanotic melanoma S91A did not measurably oxidize any of the phenols or produce browning, nor did they retard the oxidation of dopa by S91 homogenates to which they were added. Normal liver homogenates behaved like the S91A extracts.

*Cytochrome Oxidase.* In the presence of added cytochrome C, oxidation of dopa was markedly increased in the S91 melanoma homogenates, and also now occurred extensively in the S91A amelanotic melanoma and liver homogenates. This second type of dopa oxidation took place via cytochrome oxidase, not only because cytochrome C was required but because the action could be eliminated entirely by pretreatment of the homogenates with 70% ethyl alcohol, a treatment that did not decrease true dopa oxidase activity, in fact, often enhanced it, suggestive of elimination of a dopa oxidase inhibition. In no instance was tyrosine oxidized by the cytochrome system.

A third type of melanization was observed in S91AB derivatives of S91A tumors that were obtained by prolonged transfer of the latter in brown dba mice instead of white C mice. Such tumors eventually became highly pigmented, but their homogenates at this stage oxidized dopa only in the presence of added cytochrome C. However, homogenates of later transfers gradually came to show, without added cytochrome C, endogenous dopa oxidation enhanced by the alcohol treatment, indicating eventual development of true dopa oxidase activity in addition to oxidation via cytochrome oxidase. None of the amelanotic tumors, or their secondarily melanized derivatives, oxidized tyrosine except the S91AB tumor that had undergone prolonged passage (35 generations) in dba mice. In this instance oxidation was not manometrically detectable within the first 4 hours although the extracts to which tyrosine had been added blackened after ca. 24 hours.

Even though the S91AB tumor, maintained by prolonged transplantation in dba mice, assumed the enzymic pattern of the original metastatic S91 tumor, it remained biologically distinct. Thus like the original S91A amelanotic tumor, from which it was derived, it gave no evidence of producing metastases.

BIBLIOGRAPHY.

1. WOODS, M. W., DUBUY, H. G., BURK, DEAN AND HESSELBACH, MARIE. Cytological studies on the nature of the cytoplasmic particulates in the Cloudman S91 mouse melanoma. *J. N. C. Inst.*, 9: 311-323, 1949.
2. DUBUY, H. G., WOODS, M. W., BURK, DEAN AND LACKEY, MARY D. Enzymatic activities of isolated amelanotic and melanotic granules of mouse melanomas and a suggested relationship to mitochondria. *Ibid.*, 9: 325-336, 1949.
3. BURK, DEAN, ALGIRE, G. H., HESSELBACH, MARIE L., FISCHER, CLARA E. AND LEGALLAIS, FRANCES Y. Tissue metabolism of transplanted mouse melanomas, with special reference to characterization by paraphenylenediamine. Special Publications of the New York Academy of Sciences, IV, 437-446, 1948.
4. HESSELBACH, MARIE L. Cytochemical studies of certain melanotic and amelanotic mouse tumors. Master's thesis. Dept. of Chemistry, Georgetown University, Washington, D. C. May, 1949.

## Chromatographic Separation of Melanin Granules.

Vernon T. Riley, Mark Woods & Dean Burk.

*National Institutes of Health, Bethesda, Md.*

Separation of cytoplasmic particulate constituents from cells has heretofore been accomplished principally by differential centrifugation which exploits the size and specific gravity of the particles. A chromatographic system has recently been obtained which permits the separation of some of the cytoplasmic constituents from mouse melanomas by exploiting still other properties of the particulates, presumably their surface characteristics as expressed by their different adsorption affinities. By utilizing the adsorption and elution reversibility of some of the particulates, melanin granules have been separated from the Cloudman S91 and the Harding-Passey mouse melanomas in a highly active state with respect to succinoxidase, cytochrome oxidase and dopa oxidase enzyme activities. Relatively mild adsorption systems, varying between physiological saline and distilled water as the solvent extremes, and involving diatomaceous silica (Celite) columns, have been employed in order to avoid enzymic inactivation. No gross morphologic changes have been observed in the granules whether separated chromatographically or centrifugally.

A systematic study of the effects of various ions at graded concentrations in adsorbing and eluting melanin granules is under investigation, especially with reference to the possibility of obtaining granules of varying composition, either pre-existing in the tumor or induced by column passage.

The adaptation of chromatography to subcellular particulates provides a new approach to the problem of separating from the cell morphologically similar units possessing different physical or chemical surfaces.

### Bibliography.

1. Riley, Vernon T. Application of chromatography to segregation studies of the agent of chicken tumor I (Rous sarcoma virus). *Science*, 107: 573-575, 1948.
2. Riley, Vernon T., Hesselbach, Marie L., Fiala, Silvio, Woods, M. W. and Burk, Dean. Application of chromatography to the separation of subcellular, enzymatically active granules. *Science*, 109: 361-364, 1949.
3. Riley, Vernon and Woods, M. W. A short column procedure for separating cytoplasmic components from normal and tumor tissue. *Proc. Soc. Exp. Biol. & Med.*, 73:1, 92-95, 1950.

# 2.

# The Tipulidae (Order Diptera) of Rancho Grande, North-central Venezuela.[1]

Charles P. Alexander.

*Professor of Entomology, University of Massachusetts.*

(Text-figures 1-39).

[This is one of a series of papers resulting from the 45th, 46th and 47th Expeditions of the Department of Tropical Research of the New York Zoological Society, made during 1945, 1946 and 1948 under the direction of Dr. William Beebe, with headquarters at Rancho Grande in the National Park of Aragua, Venezuela. The expeditions were made possible through the generous cooperation of the National Government of Venezuela and of the Creole Petroleum Corporation.

[The characteristics of the research area are in brief as follows: Rancho Grande is located in north-central Venezuela (10° 21' N. Lat., 67° 41' W. Long.), 80 kilometers west of Caracas, at an elevation of 1,100 meters in the undisturbed montane rain forest which covers this part of the Caribbean range of the Andes. Adjacent ecological zones include seasonal forest, savanna, thorn woodland, cactus scrub, the fresh-water lake of Valencia and various marine littoral zones. The Rancho Grande area is generally subtropical, being uniformly cool and damp throughout the year because of the prevalence of the mountain cloud cap. The dry season extends from January into April. The average humidity during the expeditions, including parts of both wet and dry seasons, was 92.4%; the average temperature during the same period was 18° C; the average annual rainfall over a five-year period was 174 cm. The flora is marked by an abundance of mosses, ferns and epiphytes of many kinds, as well as a few gigantic trees. For further details, see Beebe and Crane, *Zoologica*, Vol. 32, No. 5, 1947. Unless otherwise stated, the specimens discussed in the present paper were taken in the montane cloud forest zone, within a radius of one kilometer of Rancho Grande.]

I am very greatly indebted to Dr. William Beebe and Mr. Henry Fleming, of the Department of Tropical Research of the New York Zoological Society, for the opportunity of studying a large and important series of crane-flies taken in 1945, 1946 and 1948 at and near Rancho Grande. A most interesting account of the region is provided by Dr. Beebe's recently published book, High Jungle.[2] The physiography and ecology of the area have been detailed in two important papers by Beebe and Crane.[3]

The Tipulidae of Venezuela are still very insufficiently known despite somewhat intensive collecting and study of the group during the past several years. The writer has published a total of nine reports that summarize what is known of this fauna to the year 1948. These papers bear the general title of "New or little-known Tipulidae from Venezuela (Diptera)," and were published in the *Boletin de Entomologia Venezolana,* Caracas, between 1943 and 1947, as follows:

Part I—Vol. 2: 17-26; 1943. Part II—Vol. 2: 125-144, 5 figs.; 1943. Part III—Vol. 3: 35-50, 8 figs.; 1944. Part IV—Vol. 3: 143-160, 5 figs.; 1944. Part V—Vol. 3: 171-192, 5 figs.; 1944. Part VI—Vol. 4: 59-80, 6 figs.; 1945. Part VII—Vol. 6: 37-54, 5 figs.; 1947. Part VIII—Vol. 6: 55-74, 14 figs.; 1947. Part IX—Vol. 6: 74-106, 13 figs.; 1947.

The above-cited papers record a total of 180 species of Tipulidae from Venezuela, including several from Rancho Grande that have been incorporated in the present report to assure completeness. Various additional species, not included in the paper, are from other stations in Aragua, specifically Choroni. It may be expected that several of these latter species will be found at Rancho Grande and that many further novelties may be discovered as a result of continued collecting. Despite the earlier work done at Rancho Grande, it is of interest to note that no fewer than 24 species are characterized as new at this time out of a total of 76 reported from Rancho Grande and vicinity.

I wish to express my sincere thanks to Dr. Beebe, Mr. Fleming, and others who have cooperated actively in securing the Tipulidae herein considered. I am particularly indebted to Dr. Beebe for permitting me to retain the specimens upon which this report is based, including the types of the novelties.

[1] Contribution No. 870, Department of Tropical Research, New York Zoological Society.

[2] Beebe, William. High Jungle, 379 pages (Duell, Sloan & Pearce).

[3] Beebe, William, & Jocelyn Crane.

1947. Ecology of Rancho Grande, a subtropical cloud forest in northern Venezuela. *Zoologica,* 32: 43-60, 5 pls., 10 text-figures; bibliography.

1948. Ecologia de Rancho Grande, una selva nublada subtropical en el Norte de Venezuela. *Bol. Soc. Venez. Cien. Nat.,* 11: 217-258, 5 pls., 10 text-figures.

TIPULINI.

**Brachypremna** Osten Sacken.

1. **Brachypremna dispellens** (Walker, 1860).

*Tipula dispellens* Walker; *Trans. Ent. Soc. London*, (n.s.) 5: 334; 1860.

Rancho Grande, August 27, 1944, collected by Lichy. A species having an unusually wide distribution in the New World, ranging from the United States (New Jersey, Indiana and Illinois), through Mexico and Central America to Brazil. It is known from Trinidad but is lacking elsewhere in the West Indian islands, in the Greater Antilles being replaced by *Brachypremna unicolor* Osten Sacken.

2. **Brachypremna similis** Williston, 1900.

*Brachypremna similis* Williston; Biol. Centr.-Americana, Diptera, I, Supplement: 229; 1900.

Rancho Grande, May 20, 1946. Elsewhere in Venezuela from Cano del Tigre, Merida, September, 1943 (Anduze). Type from Teapa, Tabasco, Mexico, collected by H. H. Smith. Known from Mexico, Nicaragua, Costa Rica, Panama and Venezuela.

3. **Brachypremna triangularis** Alexander, 1945.

*Brachypremna arcuaria triangularis* Alexander; *Bol. Ent. Venezolana*, 4: 60-61; 1945.

Rancho Grande, May 11-July 20, 1946; one pair taken in coitu while flying. Mt. Limon, 1500 meters, May 23, 1948. Known only from this vicinity, where the type was taken at Rancho Grande on August 27, 1944, by Lichy. Most nearly allied to *Brachypremna arcuaria* Alexander, of Amazonian Ecuador.

**Tanypremna** Osten Sacken.

4. **Tanypremna (Tanypremna) kadeni** Alexander, 1941.

*Tanypremna* (*Tanypremna*) *kadeni* Alexander; *Ann. Ent. Soc. America*, 34: 232-233; 1941.

Rancho Grande, June 24, 1945. The type was from Venezuela, without more exact geographical data, collected in August, 1857, by Carl Gotthelf Kaden. Also known from Rio Chacaito, Miranda, July 16, 1939 (Vivas-Berthier). Still known only from Venezuela.

**Holorusia** Loew.

5. **Holorusia (Holorusia) plagifera** Alexander, 1943.

*Holorusia* (*Holorusia*) *plagifera* Alexander; *Bol. Ent. Venezolana*, 2: 125-127; 1943.

Rancho Grande, March 27, 1946, ♀♀; June 22, 1946, ♂; July 18, 1946, ♂; May 3, 1948, ♂. The type was taken here on June 24, 1944, by Lichy. Still known only from the type locality.

**Nephrotoma** Meigen.

6. **Nephrotoma medioligula** Alexander, 1945.

*Nephrotoma medioligula* Alexander; *Bol. Ent. Venezolana*, 4: 69, fig. 2; 1945.

Rancho Grande, May 17, 1948, ♀; May 24, 1948, ♂; July 17, 1948, ♀. The type was taken here on August 27, 1944, by Lichy. Still known only from the type locality.

**Tipula** Linnaeus.

7. **Tipula (Bellardina) theobromina** Edwards, 1920.

*Tipula theobromina* Edwards; *Mem. Mus. Paris*, Arc de Méridien Equatorial, Dipteres Nématocères, 10 (2): 159-160, fig. 21 (ovipositor) ; 1920.

Rancho Grande, June 18, 1946, ♂. Now known from Venezuela, Ecuador, Peru and Bolivia. The type, from Ecuador, had no distinct pale ring on the femora but regional material shows such an annulus that varies in width and distinctness in different specimens. Because of the rather constant structure of the male hypopygium, I am referring all such specimens to the present species. The identity of *Tipula obliquefasciata* Macquart, 1846, still remains in question and may well be found to pertain to the present fly.

8. **Tipula (Microtipula) lichyana** Alexander, 1945.

*Tipula* (*Microtipula*) *lichyana* Alexander; *Bol. Ent. Venezolana*, 4: 71, figs. 3, 4; 1945.

Rancho Grande, May 23-June 14, 1948, migrant. The type was from here, taken May-August, 1944, by Lichy, for whom the species was named. Still known only from the type locality.

9. **Tipula (Microtipula) regressa**, sp. n.

Mesonotum obscure brownish-yellow, vaguely patterned with pale brown; antennae with flagellum black, the extreme tips of the more proximal segments restrictedly pale; wings with a weak brownish tinge, cells *C* and *Sc*, with the stigma, darker brown; male hypopygium with caudal margin of ninth tergite unequally trilobed, the lateral lobes slender, the median lobe low and broad; eighth sternite yellow, sheathing, narrowed to the broadly obtuse tip.

Male: Length about 11 mm.; wing 12 mm.; antenna about 5 mm.

Frontal prolongation of head yellow; nasus short and stout, distinct; palpi yellowish testaceous. Antennae (male) relatively long, as shown by the measurements; scape, pedicel and base of first flagellar segment yellow; flagellum black, the extreme tips of the more proximal segments restrictedly pale; flagellar segments very weakly incised, much longer than the verticils. Head with the front whitened, the posterior portions brownish-yellow, the center of the posterior vertex still darker brown; sides of vertex with numerous

black setae; vertical tubercle lacking or barely indicated.

Pronotum light brown, paling to yellow on sides. Mesonotal praescutum obscure brownish-yellow, vaguely patterned with pale brown, the markings irregular and scarcely apparent; scutum brownish-yellow; posterior sclerites of notum somewhat clearer yellow. Pleura and pleurotergite clear light yellow. Halteres with stem yellow, knob infuscated. Legs with the coxae and trochanters pale yellow; femora brownish-yellow to pale brown, the bases clear yellow; tibiae and tarsi slightly darker brown; claws (male) toothed. Wings with a weak brownish tinge. cells *C* and *Sc*, with the stigma, darker brown; prearcular field relatively pale; restricted pale areas before stigma and across cell 1*st* $M_2$; veins brown. No macrotrichia on squama or in wing cells. Venation: *Rs* gently arcuated, about one-half longer than $R_{2+3}$; vein $R_{1+2}$ entire; petiole of cell $M_1$ less than two times *m*; *m-cu* at near three-fourths the length of $M_{3+4}$; cell 2*nd A* of moderate width.

Abdomen with the basal segments obscure yellow, the third and succeeding segments chiefly infuscated, the caudal margins restrictedly pale; subterminal segments, including six, seven and base of eighth sternite dark brown to form a ring; hypopygium yellow. Male hypopygium (Text-fig. 1) with the ninth tergite, 9*t*, subequal in length and width; caudal margin unequally trilobed, including slender lateral lobes that are tipped with about four black spinous setae, and a low broad median lobe with more numerous setae; in the slide mount, these lobes are bent backward or cephalad, possibly not a natural condition; proctiger a slender pale lobe, curved and slightly enlarged at tip. Both dististyles blackened and sclerotized, shaped about as in figure *d;* beak of inner style slender, lower beak acute. Eighth sternite, 8*s*, yellow, sheathing, narrowed to the broadly obtuse tip, the outer part with pale inconspicuous setae. Appendage of ninth sternite, 9*s*, appearing as two pale elongate lobes or blades, at apex more expanded, the surface, and especially the margins, with numerous fimbriations.

Holotype, ♂, Rancho Grande, April 23, 1946 (Beebe-Fleming).

The most similar described species are *Tipula* (*Microtipula*) *inaequilobata* Alexander and *T.* (*M.*) *prolixisterna* Alexander, which differ particularly in the structure of the male hypopygia.

10. ***Tipula (Microtipula) paralenta,*** sp. n.

General coloration of thorax pale brown, the praescutum with four scarcely differentiated more brownish-yellow stripes; antennae (male) elongate, flagellar segments beyond the first black; male hypopygium with the caudal border of tergite produced into a depressed-flattened median lobe, on either side of the apex of which with about a dozen blackened spinous setae; appendage of ninth sternite appearing as two flattened divergent lobes, densely fimbriate.

Male: Length about 13.5-14 mm.; wing 13 mm.; antenna about 9.5 mm.

Frontal prolongation of head obscure yellow; nasus long and conspicuous; palpi elongate, yellow, the first segment and apex of the last a trifle more darkened. Antennae (male) elongate, as shown by the measurements; basal three segments yellow, succeeding segments black; flagellar segments elongate, very gently incised; longest verticils a little more than one-third the segments. Head brown; anterior vertex broad, about four times the diameter of the scape; orbital setae numerous, short and black, directed laterad.

Pronotum yellowish-brown. Mesonotal praescutum pale brown, with four scarcely differentiated more brownish-yellow stripes; posterior sclerites of notum more uniformly brown. Pleura and pleurotergite pale yellow, unpatterned. Halteres elongate, stem brown, knob a trifle darker. Legs with the coxae and trochanters pale yellow; femora brownish-yellow, tibiae and tarsi darker, brownish-black; claws (male) with a very small, acute tooth at near midlength. Wings with a weak brownish tinge; stigma oval, dark brown; cell *Sc* brownish-yellow; a scarcely indicated dark cloud over the anterior cord; veins dark brown. Venation: $Sc_2$ ending about opposite midlength of *Rs*, the latter subequal in length to *m-cu;* $R_{1+2}$ preserved; petiole of cell $M_1$ a little longer than *m*; basal section of $M_4$ relatively long, perpendicular; cell 2*nd A* moderately wide.

Abdominal tergites brown, the subterminal ones darker to form a more or less distinct ring; remaining sternites and the hypopygium chiefly yellow. Male hypopygium with the tergite subequal in length and breadth, the caudal margin gently concave on the central portion, very unequally trilobed; lateral lobes very slender, each tipped with one or two strong spinous setae; median lobe broad, the apex slightly produced, on either side with about a dozen similar blackened spinous setae, the actual apex glabrous. Proctiger without blackened points. Basistyle with a blackened lobe on mesal face near cephalic end. Outer dististyle a flattened lobe, narrowed at base, the tip obtuse, the surface with strong scattered setae. Inner dististyle with the beak flattened, its tip obtuse; lower beak extended into an acute point. Eighth sternite relatively short, not sheathing. Appendage of ninth sternite appearing as two separate short flattened lobes, expanded outwardly, the apex of each subtruncate; outer surface and margin with very abundant elongate fimbriations.

Holotype, ♂, La Suiza, Turrialba, Costa Rica, May, 1919 (Pablo Schild); Alexander Collection through A. L. Melander. Paratype, ♂, Mount Limon, Aragua, Venezuela, 1500 meters, May 23, 1948; (Beebe-Fleming).

The most similar of the described species

is *Tipula* (*Microtipula*) *neolenta* Alexander, 1945 (*lenta* Alexander, preoccupied), which has the antennae much shorter and with all details of the male hypopygium quite distinct. In the general features of the ninth tergite, the fly also suggests species such as *T.* (*M.*) *heterodactyla* Alexander and *T.* (*M.*) *inaequilobata* Alexander, but all other details of structure of the hypopygium are distinct.

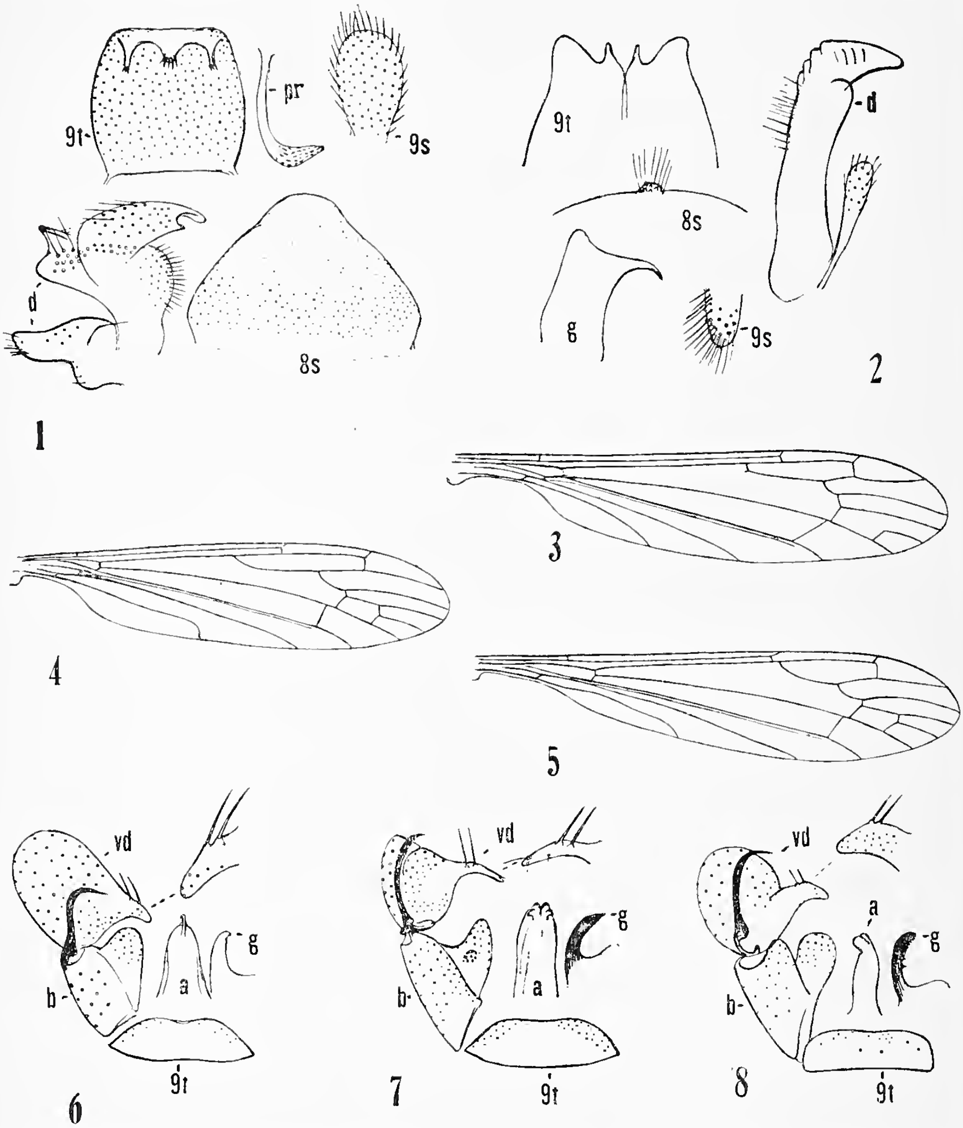
11. **Tipula (Eumicrotipula) aëdon** Alexander, 1947.

*Tipula* (*Eumicrotipula*) *aëdon* Alexander; *Bol. Ent. Venezolana*, 6:80-82, fig. 3; 1947.

Rancho Grande, August 7, 1946. Type likewise from here, taken June 10, 1945, by Lichy. Still known only from the type locality.

12. **Tipula (Eumicrotipula) andromache,** sp. n.

Size small (wing, male, 9 mm.); antennae one-third the length of wing, scape and pedicel yellow, flagellum uniformly black; mesonotum yellowish-gray, the praescutum with a broad brown median stripe; lateral stripes paler, their anterior ends curved laterad into




TEXT-FIGS. 1-8. (Symbols: *a*, aedeagus; *b*, basistyle; *g*, gonapophysis; *t*, tergite; *vd*, ventral dististyle). 1—*Tipula* (*Microtipula*) *regressa*, sp. n.; male hypopygium, details. 2—*Tipula* (*Eumicrotipula*) *araguensis*, sp. n.; male hypopygium, details. 3—*Limonia* (*Limonia*) *thamyris*, sp. n.; venation. 4—*Limonia* (*Rhipidia*) *brevipetalia*, sp. n.; venation. 5—*Limonia* (*Dicranomyia*) *serratiloba*, sp. n.; venation. 6—*Limonia* (*Limonia*) *thamyris*, sp. n.; male hypopygium. 7—*Limonia* (*Rhipidia*) *brevipetalia*, sp. n.; male hypopygium. 8—*Limonia* (*Dicranomyia*) *serratiloba*, sp. n.; male hypopygium.

the margin; legs blackened, the femora with a narrow yellow subterminal ring; claws (male) small and simple; wings cream-yellow, marbled with pale brown, cell *Sc* with four darkened areas that are more extensive than the interspaces; distal ends of outer radial cells uniformly darkened; outer cells of wing with sparse macrotrichia; male hypopygium with the tergite transverse, the caudal margin truncate, on either side of midline with a small triangular point.

Male: Length about 8 mm.; wing 9 mm.; antenna about 3 mm.

Frontal prolongation of head above light yellow, infuscated on sides and beneath; nasus distinct; palpi with basal segment dark brown, segments two and three weakly darkened basally, paler at tips, terminal segment whitened. Antennae with scape and pedicel pale yellow, the flagellum abruptly and uniformly blackened; antennae of moderate length, as shown by the measurements; flagellar segments subcylindrical, much longer than their verticils. Head above pale yellowish brown, clearer yellow on the front and anterior vertex, the latter broad, its tubercle very low and inconspicuous.

Pronotum obscure yellow medially, weakly infuscated on sides. Mesonotal praescutum with the ground yellowish-gray, with a broad brown median stripe that is more expanded in front; lateral stripes somewhat paler but extensive, at anterior ends curved laterad to the margin; posterior sclerites of notum infuscated and pruinose, the scutellum more testaceous. Pleura chiefly gray, the propleura and pteropleurite more yellowed. Halteres with stem yellow, knob infuscated. Legs with the coxae grayish, the fore pair pale yellow; trochanters yellow; femora yellowed basally, passing into brown, the tips black, preceded by a yellow ring of about one-half their width; tibiae and tarsi brownish black; claws (male) small and simple. Wings cream-yellow, marbled with pale brown; stigma and subcostal interspaces darker brown; outer portion of cell *C* infuscated, paler nearer *h;* disk of wing chiefly pale, the darkened clouds being chiefly marginal in distribution, involving the distal one-third to one-half of the outer radial cells, this part of cell $R_3$ uniformly dark; further pale brown areas crossing the disk at near midlength and again just before outer end of cells *R* and *M;* a darkened cloud over fork of $M_{1+2}$; cell *2nd A* uniformly pale brown; veins brown, yellow in the subcostal interspaces which are smaller than the four darkened areas. Sparse macrotrichia in outer ends of cells $R_3$ to $M_4$, inclusive, very restricted in cells $M_3$ and $M_4$. Venation: Compared with *immerens*, $R_{2+3}$ shorter and more oblique; cell *1st* $M_2$ smaller; *m-cu* on $M_4$ some distance beyond origin of latter; cell *2nd A* narrower.

Abdomen with the basal tergite pale, the succeeding segments brown, the subterminal segments even darker; hypopygium weakly darkened. Male hypopygium with the tergite transverse, the caudal margin truncate, on either side of midline with a small triangular point, the small area between broadly U-shaped. Outer dististyle small, with long setae. Inner dististyle with the beak elongate, pale, the shorter lower beak blackened, narrow; dorsal crest scarcely evident, weakly elevated, with pale setae and longitudinal furrows or impressed lines. Long slender dusky bladelike rods from the genital chamber appear to represent gonapophyses.

Holotype, ♂, Rancho Grande, April 24, 1948, resting on tree trunk (Beebe-Fleming); No. 4873.

Allied to *Tipula* (*Eumicrotipula*) *immerens* Alexander, likewise from Venezuela, differing in the small size, uniformly darkened antennal flagellum, and in the pattern and degree of trichiation of the wings.

13. ***Tipula (Eumicrotipula) araguensis***, sp. n.

Belongs to the *monilifera* group; mesonotum almost uniformly light cinnamon brown, the normal stripes not or poorly indicated; antennae (male) a little less than one-half the length of wing, the flagellar segments weakly bicolored; wings marbled; abdomen of male obscure orange or buffy, the basal segments very slightly patterned with darker, the subterminal segments deepening in color to form a darkened ring; male hypopygium with the tergal lobes produced into slender blades at their mesal angle; inner dististyle with the setae of the dorsal crest relatively weak, scattered, all straight; eighth sternite with the median lobe very small, low hemispherical in outline.

Male: Length about 13-14 mm.; wing 15-16.5 mm.; antenna about 7-8 mm.

Female: Length about 21-22 mm.; wing 16-17 mm.

Frontal prolongation of head light to medium brown, more pruinose at base; nasus distinct; palpi dark brown. Antennae (male) relatively long, as shown by the measurements; scape and pedicel light yellow, flagellum weakly bicolored, the stems light brown, the abrupt basal swellings brownish-black. Head light gray, with a conspicuous capillary brown vitta on vertex, the sides of the posterior vertex more extensively paler brown; vertical tubercle scarcely developed.

Mesonotum almost uniformly light cinnamon brown, more or less gray pruinose, praescutal stripes not or scarcely indicated; posterior sclerites of notum and the pleura more yellowed. Halteres with stem pale, knob infuscated. Legs brownish-yellow, the femoral tips more infuscated; remainder of legs passing through brown to dark brown. Wing of type whitish-subhyaline, with an extensive but weakly contrasted brown pattern that is arranged about as in other members of the group; the other specimens of the type series have the dark pattern much heavier and contrasted. Venation: *Rs* a little more than twice *m-cu;* tip of vein $R_{1+2}$ pale but entire;

cell *1st* $M_2$ relatively small, irregularly pentagonal; *m-cu* before fork of $M_{3+4}$; petiole of cell $M_1$ shorter than *m*.

Basal abdominal segments of male chiefly obscure orange to light brownish yellow, not or scarcely patterned, the sixth and succeeding segments deepening in color to form a dark brown ring; outer portion of hypopygium somewhat paler, brownish-yellow. In the female, abdomen more elongated; tergites with a conspicuous sublateral dark brown stripe on either side, these more widened behind. Male hypopygium (Text-fig. 2) with the tergal lobes, *9t*, at mesal angle produced into a slender flattened blade; dorsal surface of tergite furrowed. Dorsal dististyle with outer half dilated. Inner dististyle, *id*, relatively long and narrow; setae of the scarcely developed dorsal crest relatively weak, scattered, all straight, not angularly bent as in allied species. Gonapophyses, *g*, with apical lobes unequal, the lower one a slender decurved spinous point. Appendage of ninth sternite an oval lobe, the longest setae exceeding the diameter of the lobe. Eighth sternite, *8s*, transverse, the caudal margin gently and evenly convex, the median lobe very small, low-hemispherical in shape, the setae much longer than the lobe itself.

Holotype, ♂, Rancho Grande, July 18, 1946 (Beebe-Fleming). Allotopotype, ♀, May 3, 1948. Paratopotypes, 1 ♂, in copula and pinned with allotype; other ♂♀, May 9-16, 1948; paratype, of ♂, Mount Limon, 1500 meters, May 23, 1948 (Beebe-Fleming). One pair, taken in copula, were resting on the exposed root of a tree growing on a steep bank.

There are several similar regional members of the *monilifera* group, including *Tipula* (*Eumicrotipula*) *chacopata* Alexander, *T.* (*E.*) *inaequidens* Alexander, *T.* (*E.*) *infinita* Alexander, and *T.* (*E.*) *palenca* Alexander, all of which differ from the present species and among themselves in the structure of the male hypopygium, particularly the tergite, inner dististyle, gonapophysis and lobe of the eighth sternite.

14. **Tipula (Eumicrotipula) cristata** Alexander, 1945.

*Tipula* (*Eumicrotipula*) *cristata* Alexander; *Bol. Ent. Venezolana*, 4: 72-74, fig. 5; 1945.

Rancho Grande, September 13, 1944, collected by Lichy; types. Still known only from the type locality.

15. **Tipula (Eumicrotipula) infinita** Alexander, 1945.

*Tipula* (*Eumicrotipula*) *infinita* Alexander; *Bol. Ent. Venezolana*, 4: 76-78, fig. 6; 1945.

Rancho Grande, April, 1944, collected by Lichy; type. Still known only from the type locality.

16. **Tipula (Eumicrotipula) tovarensis** Alexander, 1947.

*Tipula* (*Eumicrotipula*) *tovarensis* Alexander; *Bol. Ent. Venezolana*, **6**: 40-42, fig. 1; 1947.

Rancho Grande, August 24, 1944, collected by Lichy. Still known only from the type locality.

### LIMONIINI.

### **Limonia** Meigen.

17. **Limonia (Limonia) alfaroi** (Alexander, 1922).

*Dicranomyia alfaroi* Alexander; *Proc. U. S. Nat. Mus.*, 60, Art. 25: 2-3; 1922.

Rancho Grande, Aug. 8, 1946. The type was from San José, Costa Rica, taken October 7, 1920, by Alfaro. The typical form of the species ranges from southern Mexico to Venezuela.

18. **Limonia (Limonia) fumosa** (Alexander, 1912).

?*Furcomyia fumosa* Alexander; *Can. Ent.*, 44: 364, fig.; 1912.

Rancho Grande, June 9, 1937, collected by Vivas-Berthier. The type was taken at Amatuk, British Guiana, July 14, 1911, by F. E. Lutz. Still known only from Venezuela and British Guiana.

19. **Limonia (Limonia) onoma**, sp. n.

Thoracic pleura yellow, with a broad brown longitudinal stripe; front of head silvery, the posterior part dark brownish-gray; legs dark brown; wings subhyaline, conspicuously patterned with brown, including a quadrate area at origin of *Rs*, stigma and broad seams over cord and outer end of cell *1st* $M_2$; no darkening at arculus but with one at near one-fourth the length of cell *R*; $Sc_1$ ending about opposite midlength of *Rs*; basal section of vein $R_{4+5}$ angulated; vein *2nd A* bent strongly into the margin.

Female: Length about 7 mm.; wing 8.3 mm.; antenna about 1.5 mm.

Rostrum black; palpi brownish-black. Antennae black throughout; basal flagellar segments short-subcylindrical, the outer ones passing through oval to elongate; terminal segment nearly twice as long as the penultimate; longest verticils unilaterally arranged, exceeding the segments, excepting the terminal one. Head dark brownish-gray; front and anterior vertex silvery, the latter reduced to a linear strip.

Pronotum brownish-yellow. Mesonotum light brown, the lateral portions of praescutum restrictedly paler. Pleura yellow, with a broad brown longitudinal stripe extending from the cervical region to the base of abdomen, passing beneath the root of halteres. Halteres brown, base of stem restrictedly brightened, knob brownish-black. Legs with all coxae and trochanters pale yellow; remainder of legs dark brown, the femoral bases not or scarcely brightened. Wings with the ground subhyaline, with a conspicuous brown pattern that includes a quadrate area at origin of *Rs*, stigma, and broad seams

over cord and outer end of cell 1*st* $M_2$; other darkenings include a circular area over fork of *Sc*, not touching the one at origin of *Rs;* spots at ends of both Anal veins, that at 2*nd A* larger; a cloud at about one-fourth the length of cell *R*, in transverse alignment with the end of vein 2*nd A;* no darkening at arculus; small marginal clouds on veins $R_3$, $R_{4+5}$, $M_3$, $M_4$ and *Cu*, scarcely evident on the veins near wing-tip; in outer radial field with a narrow subapical cloud in cells $R_2$ and $R_3$; veins brown, *Sc* brighter. Venation: *Sc* long, $Sc_1$ ending beyond midlength of *Rs*, $Sc_2$ near its tip; *Rs* long, square at origin; inner end of cell $R_2$ lying basad of that of 1*st* $M_2$, the basal section of $R_{4+5}$ being angulated; cell 1*st* $M_2$ elongate, subequal to vein $M_{1+2}$ beyond it; *m-cu* at fork of *M*, longer than the distal section of $Cu_1$; vein 2*nd A* bent strongly into the wing margin.

Abdomen dark brown, the sternites a trifle paler. Ovipositor with cerci slender, upcurved; hypovalvae longer and straight.

Holotype, ♀, Rancho Grande, May 12, 1946 (Beebe-Fleming).

The most similar regional species are *Limonia* (*Limonia*) *eiseni* (Alexander) and *L.* (*L.*) *macintyrei* Alexander, both of which are quite distinct in the wing pattern and details of venation.

20. **Limonia (Limonia) pampoecila** (Alexander, 1922), var.

*Dicranomyia pampoecila* Alexander; *Proc. U. S. Nat. Mus.*, 60, Art. 25: 1-2; 1922.

Rancho Grande, June 28, 1946; a fragmentary female. Close to the typical form but with the darkened femoral ring terminal in position whereas in typical *pampoecila* this is subterminal. The material is too poor for more exact determination. The type of *pampoecila* was from Tiribi, Costa Rica, collected October 9, 1920, by Alfaro. What appears to represent a single species ranges from Costa Rica to southeastern Brazil but this complex requires further study.

21. **Limonia (Limonia) thamyris**, sp. n.

General coloration gray, patterned with brown, the markings on the praescutum irregular in distribution; femora black, yellow basally, with a very narrow and indistinct yellow subterminal ring; wings whitish-subhyaline, with a heavy reticulated brown pattern; cell $M_2$ open by the atrophy of *m;* male hypopygium with the ventral dististyle large and fleshy, its rostrum with two long spines, the more proximal one from a small basal tubercle.

Male: Length about 5.5 mm.; wing 6 mm.

Rostrum brownish-black, sparsely pruinose; palpi black; rostrum in direct alignment with the front. Antennae with the short scape black, pedicel light yellow; flagellum black, the first segment paler; flagellar segments oval, slightly longer than the verticils. Head buffy brown, more pruinose medially behind, the center of the posterior vertex with a blackened area.

Pronotum brownish-yellow, pruinose. Mesonotal praescutum with the ground grayish pruinose, patterned irregularly with dark brown, the broader median stripe entire on the posterior third, in front branching into four narrow lines; lateral stripes similarly narrow; scutal lobes dark brown, the median area narrowly more silvery, the line continued caudad onto the scutellum; remainder of the latter brown, margined with darker brown; central portion of mediotergite dark brown, the lateral margins yellow. Pleura and pleurotergite striped longitudinally with brownish-yellow and dark brown, the surface pruinose to produce a variegated effect. Halteres with stem yellow, knob dark brown. Legs with the coxae obscure yellow, the fore pair darkened basally; trochanters obscure yellow, the fore pair darkened apically; femora obscure yellow on about the proximal third or fourth, the remainder brownish-black, enclosing a very narrow and indistinct obscure yellow ring some distance back from the blackened tip; tibiae dark brown; tarsi more yellowish-brown, the outer segments blackened, the posterior tarsi more uniformly so; claws (male) with a strong, nearly basal spine, with a smaller acute point still more basad. Wings (Text-fig. 3) with the restricted ground whitish-subhyaline, with a heavy reticulated brown pattern, paler brown in the apical and posterior cells of wing; cell *Sc* and the prearcular field more yellowed; a series of about a dozen brown dashes in cell *C*, narrower than the interspaces, cell *Sc* clearer yellow; three major darker brown areas in cell *R*, the first postarcular, the third at origin of *Rs;* a similar slightly paler brown cloud in cell *M* just before the level of origin of *Rs;* further major areas at stigma and anterior cord and near the outer end of vein $R_3$; reticulated areas in apical and posterior cells paler and few in number but distinct; veins brown, *Sc* and *R* more yellowed. Venation: *Sc* moderately long, $Sc_1$ ending just before midlength of *Rs*, $Sc_2$ at its tip; *Rs* angulated and short-spurred at origin; vein $R_3$ slightly arcuated on basal half; cell $M_2$ open by atrophy of *m; m-cu* shortly before fork of *M*, long and very oblique, about one-fourth longer than the distal section of vein $Cu_1$.

Abdomen brown, the hypopygium yellowed. Male hypopygium (Text-fig. 6) with the tergite, 9*t*, transverse, the caudal margin very gently emarginate, the low lateral lobes with long pale setae. Basistyle, *b*, with the ventromesal lobe large, obtuse at apex. Dorsal dististyle a strong rod, the long apical spine nearly straight. Ventral dististyle, *vd*, large and fleshy, its area about one-third greater than the total of the basistyle; rostral prolongation stout, the two spines relatively long, subequal in length, placed one behind the other, the more basal one from a slightly larger tubercle. Gonapophysis, *g*, with mesal-apical lobe elongate, pale, terminating in a small darkened knob that is directed laterad.

Holotype, ♂, Rancho Grande, June 27, 1946 (Beebe-Fleming).

Generally similar to *Limonia* (*Limonia*) *pampoecila* (Alexander) and certain allied species, differing in the pattern of the legs and wings, the venation, especially the open cell $M_2$, and in the details of structure of the male hypopygium.

22. **Limonia (Neolimnobia) diva** (Schiner, 1868).

*Limnobia diva* Schiner; Novara Reise, Diptera, p. 46; 1868.

Rancho Grande, May 7-11, 1946, August 1-7, 1946; also September 5, 1942, collected by Lichy. Specimens taken between July 10 and 18, 1946, have the pattern of the femora much obscured, as noted below.

The species *diva*, as now restricted, has a wide range in tropical America, including the Greater Antilles (Cuba, Puerto Rico), Mexico, Venezuela and Brazil. Further races or closely allied species are found in Ecuador and Peru. The variability in the distinctness of the leg pattern in what seems to represent a single species has been discussed by the writer in another paper (Notes on the Tropical American species of Tipulidae (Diptera). VI. *Rev. de Entomologia—in press*). As there indicated, some individuals have two or, in cases, three dark rings on the femora while other specimens that are referred to *diva* without question have the femoral pattern much obscured, the darkened annuli being broader and more diffuse, in the extreme cases being so vague and extensive as to eliminate the yellow interspaces. The extreme specimens from Rancho Grande above mentioned do not quite represent the condition described but individuals from elsewhere in Venezuela have this leg pattern.

23. **Limonia (Rhipidia) brevipetalia**, sp. n.

Praescutum reddish-brown, with indications of darker lines and dashes; pleura and pleurotergite more gray pruinose, narrowly lined with darker; antennae dark, the two subterminal segments white; flagellar segments short-bipectinate; femora darkened subterminally, the actual tip narrowly yellow; wings pale yellow, with a very abundant pale brown dotted pattern, the marks chiefly confluent; male hypopygium with the caudal margin of the tergite very gently emarginate; rostral prolongation of the ventral dististyle unusually long and slender, the two spines subequal in length and size.

Male: Length about 7 mm.; wing 8 mm.

Rostrum brownish-black, shiny, the mouthparts conspicuous; palpi black. Antennae black, the long pedicels of the flagellar segments pale yellow; subterminal two segments whitened; flagellar segments one to three strongly produced but simple; segments four and five each with two conspicuous branches that slightly exceed in length the remainder of organ (the succeeding segments broken, the color pattern having been noted before the breakage occurred). Head dark gray; anterior vertex reduced to a linear strip that does not exceed in width two rows of ommatidia.

Pronotum dark brown, the scutellum and pretergites more reddish-brown. Mesonotal praescutum chiefly reddish-brown, with indications of dark lines and dashes, as well as the posterior end of the usual median stripe; scutal lobes dark; scutellum yellowish-gray with a black central line; mediotergite gray pruinose, the central part more heavily so, the lateral borders paling to yellow. Pleura and pleurotergite gray pruinose, narrowly lined longitudinally with dark brown, the dorsal stripe most conspicuous, the ventral line a short dash on the sternopleurite; the dorsal stripe begins at the propleura, narrowed behind at the root of the halteres. Halteres with stem dirty white, more yellowed at base, knob infuscated. Legs with the coxae brown, pale at tips; trochanters yellow; femora light brown, paler basally, deepening to a somewhat more intense subterminal ring, the actual tip narrowly yellow; tibiae and tarsi obscure yellow, the terminal two segments black; claws (male) with a strong subbasal spine, with a smaller one a little more basad. Wings (Text-fig. 4) with the restricted ground pale yellow, with a very abundant pale brown dotted pattern, the areas being so abundant as to be extensively confluent; very small darker dots beyond midlength of vein *R*, origin of *Rs*, and fork of *Sc;* cord and outer end of cell 1*st* $M_2$ narrowly seamed with darker; a more or less evident series of two or three brown spots along vein *Cu* in cell *M;* veins yellow, variegated with darker in the more heavily patterned areas. Venation: $Sc_1$ ending opposite or just beyond midlength of *Rs*, $Sc_2$ at its tip; *m-cu* more than one-third its length before the fork of *M*.

Abdominal tergites reddish-brown, the lateral borders narrowly blackened; sternites a trifle more yellowed; hypopygium and segment eight yellow. Male hypopygium (Text-fig. 7) with the tergite, 9*t*, transverse, the caudal margin very gently emarginate, the surface of the low lobes with abundant setae. Basistyle, *b*, subequal in area to the ventral dististyle, the ventromesal lobe large, with a small lateral lobule. Dorsal dististyle a gently curved blackened rod, the tip acute. Ventral dististyle, *vd*, with the rostrum unusually long and slender, the two spines slightly separated, the outermost at near midlength of the prolongation; spines straight, subequal in size. Gonapophysis, *g*, with the mesal-apical lobe stout, gently curved, heavily blackened, the tip acute or subacute. Aedeagus, *a*, stout.

Holotype, ♂, Rancho Grande, June 7, 1946 (Beebe-Fleming).

In its abundantly dotted wings, the present fly most resembles species such as *Limonia* (*Rhipidia*) *monoxantha* Alexander, which differs conspicuously in the coloration and in the wing pattern. The male sex of *monoxantha* is still unknown.

24. **Limonia (Rhipidia) domestica** (Osten Sacken, 1859).

*Rhipidia domestica* Osten Sacken; *Proc. Acad. Nat. Sci. Philadelphia*, 1859: 208, pl. 3, figs. 8-9; 1859.

Rancho Grande, June 26-28, July 10, August 3, 1946.

Described from the eastern United States; very widely distributed, ranging from Connecticut, New York and New Jersey, southward throughout the southern states; Antilles (Cuba, Jamaica, Puerto Rico, Lesser Antilles); Venezuela; Brazil.

25. **Limonia (Rhipidia) flabelliformis** Alexander, 1934, var.

*Limonia (Rhipidia) flabelliformis* Alexander; *Ann. Ent. Soc. America*, 27: 59-60; 1934.

Rancho Grande, May 29, 1946. The type was from Chiriqui, Panama, altitude 5400 feet, taken September 13, 1932, by Lawlor. The typical form ranges from Panama to Peru.

26. **Limonia (Dicranomyia) brevicubitalis** Alexander, 1947.

*Limonia (Dicranomyia) brevicubitalis* Alexander; *Bol. Ent. Venezolana*, 6: 87-90, figs. 7, 8; 1947.

Rancho Grande, May 5, June 16-28, July 23, 1946; May 13, 1948. Type from the Rio Chacaito, Miranda, Venezuela, 980 meters, September 18, 1938, collected by Vivas-Berthier. Other specimens from Los Venados, D. F., 1520 meters, February 26, 1939, Vivas-Berthier. Still known only from Venezuela.

27. **Limonia (Dicranomyia) brevivena capra** Alexander, 1947.

*Limonia (Dicranomyia) capra* Alexander; *Bol. Ent. Venezolana*, 6: 57-59, figs. 1, 5; 1947.

Rancho Grande, April 21, 1946. Type from here, collected by Lichy on August 27, 1944. Elsewhere in Venezuela known from the Rio Chacaito, Miranda, 980 meters, September 18, 1938, Vivas-Berthier; Los Canales, Naiguata, D. F., 720 meters, September 24, 1938, Vivas-Berthier.

I am considering this as representing a race of the more northern and unusually widespread *brevivena* (Osten Sacken, 1869).

28. **Limonia (Dicranomyia) serratiloba**, sp. n.

Allied to *mutata;* general coloration gray, the praescutum and scutal lobes extensively more infuscated; legs chiefly black, the femoral bases obscure yellow; wings with a strong brownish tinge, the very small subcircular stigma darker brown; male hypopygium with the tergite narrowly transverse, the caudal margin nearly truncate; rostral prolongation of the ventral dististyle stout, the two spines relatively short, straight, from small basal tubercles; mesal-apical lobe of the gonapophysis long and slender, the margin with conspicuous serrulations.

Male: Length about 5.5 mm.; wing 6 mm.

Rostrum and palpi brownish-black. Antennae black throughout; flagellar segments oval. Head gray; anterior vertex very narrow, reduced to a linear strip.

Pronotum brownish-gray. Mesonotum chiefly dark brownish-gray, the praescutum and scutal lobes extensively more infuscated. Pleura blackened, heavily pruinose. Halteres relatively long, stem dirty white, knob infuscated. Legs with the coxae dark brown, sparsely pruinose; trochanters obscure yellow; femora obscure yellow basally, passing into black; remainder of legs black; claws (male) with at least two basal teeth, the outermost strongest. Wings (Text-fig. 5) with a strong brownish tinge, the very small subcircular stigma darker brown; exceedingly vague and narrow seams over the cord; prearcular field a little more whitened; veins brown. Venation: $Sc_1$ ending opposite origin of $Rs$, $Sc_2$ near its tip; $Rs$ slightly more than twice as long as the more arcuated basal section of $R_{4+5}$; cell 1*st* $M_2$ a trifle longer than vein $M_4$; *m-cu* a short distance before the fork of $M$.

Abdomen, including hypopygium, dark brown. Male hypopygium (Text-fig. 8) with the tergite, 9*t*, narrowly transverse, the caudal margin nearly truncate; scattered pale setae along the margin, with an additional discal pair. Basistyle, *b*, with the ventromesal lobe large, obtuse, provided with long yellow setae. Dorsal dististyle a curved blackened rod, narrowed very gradually into a long acute spine. Ventral dististyle, *vd*, fleshy, its total area somewhat greater than that of the basistyle; rostral prolongation stout, its tip obtuse; rostral spines two, arising from equal small tubercles, the spines straight and relatively short. Gonapophysis, *g*, with the blade pale, the mesal-apical lobe long and slender, gently curved, the margin with several conspicuous serrulations.

Holotype, ♂, Rancho Grande, June 16, 1946 (Beebe-Fleming).

The present fly is generally similar to species such as *Limonia (Dicranomyia) mutata* Alexander, differing in the coloration of the body and wings and in the structure of the male hypopygium, particularly the tergite, ventral dististyle and gonapophyses.

29. **Limonia (Peripheroptera) angustifasciata** (Alexander, 1922).

*Peripheroptera angustifasciata* Alexander; *Trans. Ent. Soc. London*, 1922: 35-36; 1922.

Rancho Grande, April 17-27, June 25, July 15, 1946; July 10, 1945; March 26, 1948. Two further specimens of the migrant series, May 23, 1948, ♀ (No. 48569) and July 21, 1948, ♂ (No. 481275).

The type was from "Venezuela," with no further data, contained in the collection of the Vienna Museum and to this time no further specimens had been taken. The wings in

the present series agree well with those of the type female except in the sexual characters, as found in most species in the subgenus *Peripheroptera* Schiner. I regard the identification as correct.

30. **Limonia (Geranomyia) callinota** Alexander, 1941.

*Limonia (Geranomyia) callinota* Alexander; *Ann. Mag. Nat. Hist.*, (11) 8: 318-320; 1941.

Rancho Grande, June 28, 1946; 1 ♀. The type was from Carpapata, Junin, Peru, 2600 meters, May 15, 1940, collected by Woytkowski. Known only from these two stations. I see no reason to question the present determination even though it is based on the female sex.

31. **Limonia (Geranomyia) furor** Alexander, 1944.

*Limonia (Geranomyia) furor* Alexander; *Bol. Ent. Venezolana*, 3: 183-185, fig. 5; 1944.

Rancho Grande, June 26, 1946. Type from Rio Chacaito, Miranda, Venezuela, 980 meters, September 18, 1938, Vivas-Berthier. Still known only from Venezuela.

32. **Limonia (Geranomyia) opinator**, sp. n.

Size small (wing, male, 5.5 mm.); rostrum relatively short; praescutum light gray, with three brown stripes additional to the darkened lateral borders; femora with a narrow brown subterminal ring; wings grayish-subhyaline, with a very restricted darker pattern, including a common cloud over the origin of *Rs* and fork of *Sc;* male hypopygium with the ventral dististyle large and fleshy, the prolongation slender, with two spines that arise from slightly unequal tubercles; gonapophysis with mesal-apical lobe a slender pale horn.

Male: Length, excluding rostrum, about 5 mm.; wing 5.5 mm.; rostrum about 2.5 mm.

Rostrum of moderate length, approximately one-half the remainder of body, brownish-black throughout. Antennae black, relatively short; flagellar segments oval, with short verticils. Head gray, the posterior vertex with a dark brown longitudinal stripe on either side of the subequal median ground line.

Pronotum buffy, weakly infuscated medially and on the sides. Mesonotal praescutum light gray, with three dark brown stripes on the disk, the intermediate pair convergent behind and becoming confluent at the suture, the shorter median stripe becoming obsolete some distance before the suture; lateral praescutal borders less heavily darkened, humeral region yellowed; scutum chiefly brownish-gray, including the lobes; posterior sclerites of notum dark brown, pruinose. Pleura with a dark brown dorsal stripe, the ventral pleurites yellow. Halteres with stem obscure yellow, its base brighter, knob dark brown. Legs with the coxae yellow, the fore pair with the basal half darkened; trochanters yellow; femora obscure yellow, passing into light brown outwardly, with a narrow darker brown subterminal ring, subequal in extent to the yellow tip; tibiae and tarsi pale, the outer tarsal segments dark brown; claws slender, with a single strong basal spine. Wings (Text-fig. 9) grayish-subhyaline, the prearcular and narrow costal region more yellowed; a very restricted dark pattern, including the stigma; a small common cloud over the origin of *Rs* and fork of *Sc;* and vague narrow seams over the cord and outer end of cell 1st $M_2$; veins brown, pale in the yellowed areas. Venation: *Sc* short, $Sc_1$ ending immediately beyond the origin of *Rs*, $Sc_2$ opposite this origin; cell 1st $M_2$ long, nearly equal to the distal section of vein $M_{1+2}$; *m-cu* shortly beyond the fork of *M*.

Abdomen, including hypopygium, dark brown. Male hypopygium (Text-fig. 16) with the tergite, *9t*, transverse, the caudal border broadly emarginate, the relatively low lateral lobes with numerous long coarse setae. Basistyle, *b*, small, its total area a little less than one-third that of the ventral dististyle; ventromesal lobe simple. Dorsal dististyle a slender curved rod, the slightly upcurved tip acute. Ventral dististyle, *vd*, large and fleshy; rostral prolongation slender, the two spines straight, slightly unequal in length from tubercles of unequal size, the longer spine lying more basad on the longer tubercle. Gonapophysis, *g*, with the mesal-apical lobe a slender nearly straight pale horn. Aedeagus, *a*, with apical lobes obtuse.

Holotype, ♂, Rancho Grande, June 26, 1946 (Beebe-Fleming).

While generally similar to species such as *Limonia (Geranomyia) recisa* (Alexander), the present fly differs evidently in the structure of the male hypopygium.

33. **Limonia (Geranomyia) stenophallus** Alexander, 1944.

*Limonia (Geranomyia) stenophallus* Alexander; *Ann. Ent. Soc. America*, 37: 310-311; 1944.

Rancho Grande, June 26, 1946. The type was from Abitagua, Ecuador, 1100 meters, March 21, 1940, collected by Macintyre. The species ranges from Venezuela to Ecuador and Peru.

34. **Limonia (Geranomyia) subvirescens** Alexander, 1930.

*Limonia (Geranomyia) subvirescens* Alexander; *Journ. N. Y. Ent. Soc.*, 38: 112; 1930.

Rancho Grande, July 23, 1946. The type was from the Trinidad Mountains, Cuba, 1000 feet, taken March 25, 1925, by J. G. Myers. Ranges from the Greater Antilles (Cuba) to Venezuela.

35. **Limonia (Geranomyia) tibialis** (Loew, 1851).

*Aporosa tibialis* Loew; *Linnea Entomologica*, 5: 397; 1851.

Rancho Grande, July 5-31, 1946. The type was from Brazil, without further data, collected by Sellow. This is one of the most

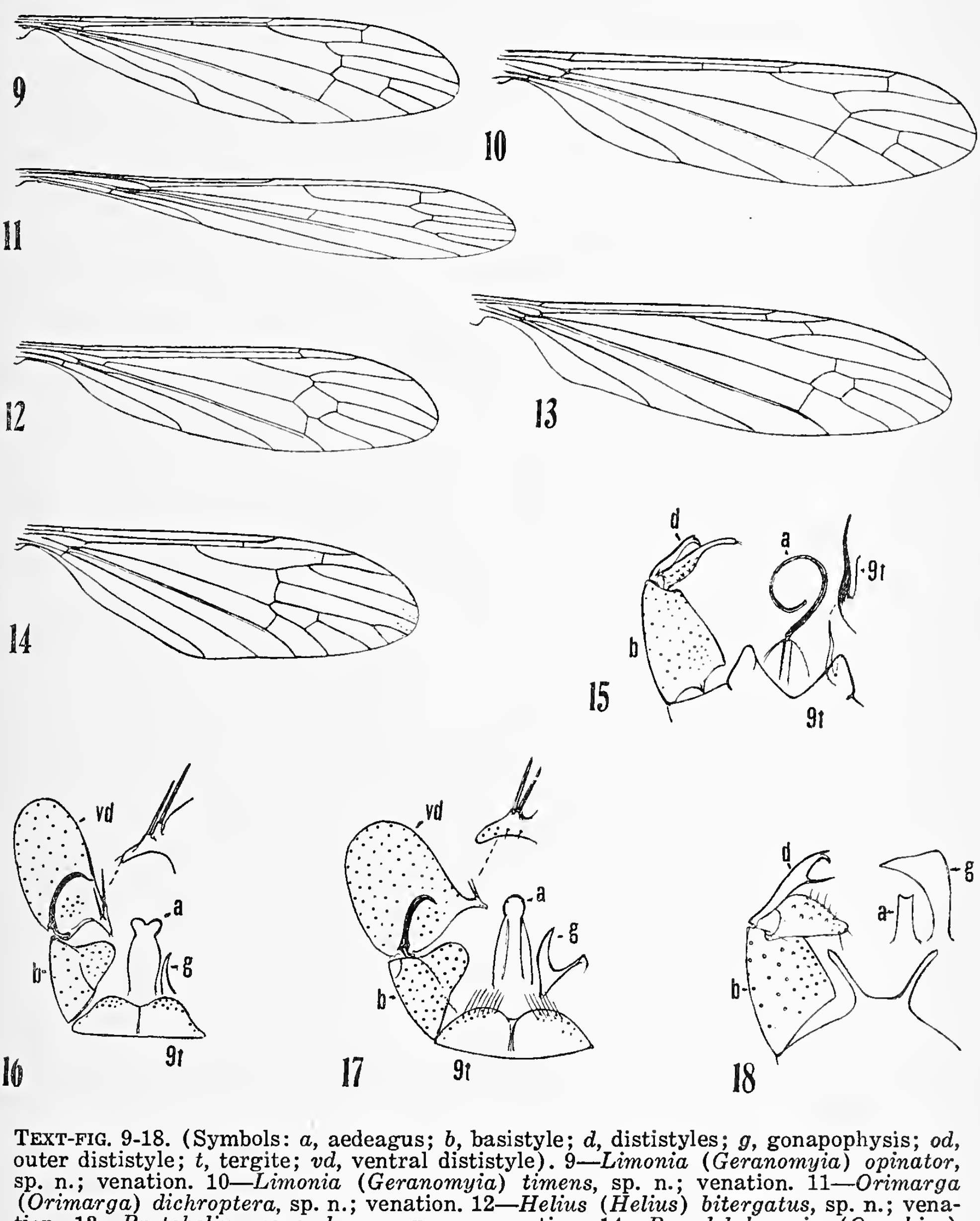
widely distributed of all tropical American Tipulidae, ranging from the Greater Antilles (Jamaica, Puerto Rico); Lesser Antilles (Dominica, Grenada); Central America; British Guiana, into Paraguay. It may be noted that this is the only species of cranefly so far taken on the Galápagos Islands.

36. ***Limonia (Geranomyia) timens***, sp. n.

Size small (wing under 6 mm.); rostrum short, only a little more than one-third the length of wing; praescutum gray with three narrow brown stripes, additional to the paler sublateral darkening; femora with a very poorly indicated pale brown subterminal ring; wings weakly tinged with brown, with a very restricted pale brown pattern, including a common area over the origin of *Rs* and fork of *Sc;* male hypopygium with the ventral dististyle large and fleshy, the prolongation relatively short but slender, more or less constricted basad of the spines, the latter arising from strong tubercles.

Male: Length, excluding rostrum, about 5 mm.; wing 5.8 mm.; rostrum about 2.1 mm.

Rostrum short, only a little more than one-




Text-fig. 9-18. (Symbols: *a*, aedeagus; *b*, basistyle; *d*, dististyles; *g*, gonapophysis; *od*, outer dististyle; *t*, tergite; *vd*, ventral dististyle). 9—*Limonia (Geranomyia) opinator*, sp. n.; venation. 10—*Limonia (Geranomyia) timens*, sp. n.; venation. 11—*Orimarga (Orimarga) dichroptera*, sp. n.; venation. 12—*Helius (Helius) bitergatus*, sp. n.; venation. 13—*Protohelius venezolanus*, sp. n.; venation. 14—*Paradelphomyia (Oxyrhiza) venezolana*, sp. n.; venation. 15—*Helius (Helius) bitergatus*, sp. n.; male hypopygium. 16—*Limonia (Geranomyia) opinator*, sp. n.; male hypopygium. 17—*Limonia (Geranomyia) timens*, sp. n.; male hypopygium. 18—*Paradelphomyia (Oxyrhiza) venezolana*, sp. n.; male hypopygium.

third the length of the wing, black throughout. Antennae black; flagellar segments subcylindrical, with inconspicuous verticils. Head above gray, with a blackish line on either side of the median ground line of the posterior vertex.

Pronotum buffy gray, dark brown medially. Mesonotal praescutum gray, with three narrow but conspicuous intermediate dark brown stripes that are subequal in width and nearly twice as broad as the interspaces; sublateral stripes broader but less intense than the three central ones; posterior sclerites of notum gray, each scutal lobe with two darkened areas. Pleura chiefly pale reddish-brown, the surface vaguely pruinose, the more ventral portions paler. Halteres with stem pale, knob dark brown. Legs with the coxae and trochanters pale yellow; femora yellow, with a narrow and very poorly indicated pale brown subterminal ring, the yellow apex subequal in extent; remainder of legs brownish-yellow, the tarsi not or scarcely darkened. Wings (Text-fig. 10) with a weak brownish tinge, the prearcular field and relatively broad costal border more yellowed, the latter pattern continued almost to the wing tip; a very restricted pale brown pattern, including the stigma, a smaller common area over the origin of *Rs* and fork of *Sc*, and a still smaller cloud at the supernumerary crossvein in cell *Sc;* veins brownish-yellow, slightly darker in the patterned areas. Venation: *Sc* relatively short, $Sc_1$ ending about opposite one-third the length of *Rs*, $Sc_2$ a short distance back from tip; *r-m* reduced in length by the approximation of veins $R_{4+5}$ and $M_{1+2}$; cell 1*st* $M_2$ slightly longer than vein $M_3$; *m-cu* at fork of *M*.

Abdomen, including hypopygium, pale yellowish-brown. Male hypopygium (Text-fig. 17) with the tergite, 9*t*, transverse, the caudal border with a median notch to form two low rounded lobes that are provided with abundant long setae. Basistyle, *b*, relatively small, its total area about one-third that of the ventral dististyle; ventromesal lobe simple. Dorsal dististyle a gently curved rod, the tip gradually narrowed into a slender spine. Ventral dististyle, *vd*, large and fleshy, the rostral prolongation relatively short but slender, more or less constricted basad of the spines; spines two, from strong tubercles, slightly unequal in length, the shortest subequal in length to the prolongation. Gonapophysis, *g*, with the mesal-apical lobe pale, appearing as a gently curved flattened horn, the tip acute.

Holotype, ♂, Rancho Grande, June 26, 1946 (Beebe-Fleming).

Related to species such as *Limonia* (*Geranomyia*) *recisa* Alexander, *L.* (*G.*) *scolopax* (Alexander) and *L.* (*G.*) *opinator*, sp. n., differing from all chiefly in the structure of the male hypopygium.

37. **Limonia (Geranomyia) vindicta** Alexander, 1943.

*Limonia* (*Geranomyia*) *vindicta* Alexander; *Bol. Ent. Venezolana,* **2**: 21-22; 1943.

Rancho Grande, May 10, 1946. Type from Rio Chacaito, Miranda, Venezuela, 980 meters, September 18, 1938, collected by Vivas-Berthier. The typical form is still known only from Venezuela; the race, *dilucida* Alexander, from Ecuador.

38. **Limonia (Geranomyia) walkeri** Alexander, 1930.

*Limonia* (*Geranomyia*) *walkeri* Alexander; *Ann. Ent. Soc. America,* 23: 730-732; 1930.

Rancho Grande, September 5, 1937, Vivas-Berthier. The type was from Vista Nieve, Mount Santa Marta, Colombia, 5000 feet, August 8, 1926, collected by Fred W. Walker. Other typical material from Jaragua, Santa Catharina, Brazil, August 29, 1929. The species occurs from Colombia and Venezuela to southeastern Brazil.

### **Orimarga** Osten Sacken.

39. **Orimarga (Orimarga) dichroptera,** sp. n.

Allied to *niveitarsis;* general coloration black, the sides of the thorax with two narrow silvery longitudinal stripes; legs black, the femoral bases of the middle and hind legs yellowed; tarsi extensively white; wings strongly bicolored, the cephalic half brownish-black, the posterior half and the prearcular field whitened; vein *Sc* short, $Sc_1$ ending some distance before origin of *Rs;* cell $M_3$ approximately twice its petiole; vein 2*nd A* short; abdomen elongate.

Female: Length about 9.5-10 mm.; wing 5.5 mm.; abdomen alone 7.5-8 mm.

Rostrum and palpi black. Antennae black throughout, short; flagellar segments oval. Head above black, sparsely dusted with gray.

Thoracic dorsum black, the praescutum with a narrow silvery gray longitudinal stripe. Pleura black, with a slightly broader silvery gray longitudinal stripe, extending from the cephalic portion of the sternopleurite to the abdomen. Halteres black. Legs with the fore coxae and trochanters black, the remaining coxae black basally, their apices broadly yellow; trochanters yellow; fore legs black, middle and posterior legs black, the femoral bases extensively yellow; outer two-fifths of basitarsi and remainder of tarsi excepting the last segment snowy white. Wings (Text-fig. 11) strongly bicolored, the cephalic half brownish-black, the posterior part more whitened; darkened areas include the anterior third of wing, most of cells *R* and *M*, bases of *Cu* and 1*st A*, and all of cell 2*nd A;* prearcular field chiefly white; veins brownish-black. Venation: *Sc* short, $Sc_1$ ending a distance before origin of *Rs* greater than the length of *m-cu*, the latter opposite the base of *Rs;* $R_{2+3}$ and $R_2$ subequal, about one-half $R_{1+2}$; inner end of cell $R_5$ a little more distad than those of cells $R_3$ and

$M_2$; cell $M_3$ about one and one-half to two times its petiole; vein *2nd A* short.

Abdomen elongate, black; valves of ovipositor horn-yellow.

Holotype, ♀, Rancho Grande, July 9, 1946 (Beebe-Fleming). Paratopotype, 1 ♀.

Readily distinguished from *Orimarga* (*Orimarga*) *niveitarsis* Alexander, and its larger race *majuscula* Alexander, by the strongly bicolored wings, with the venational details distinct.

40. **Orimarga (Orimarga) excessiva** Alexander, 1926.

*Orimarga* (*Orimarga*) *excessiva* Alexander; *Ann. Ent. Soc. America*, 19: 380-381; 1926.

Rancho Grande, May 10, June 26-28, 1946. Type from Tachira, Venezuela, April 4, 1920, Williamsons & Ditzler. Still known only from Venezuela.

### **Helius** St. Fargeau.

41. **Helius (Helius) bitergatus,** sp. n.

Praescutum and scutal lobes brown; posterior sclerites of notum and the pleura lighter brown; legs dark brown, the outer tarsal segments paling to yellowish-brown; wings with a strong brownish tinge, stigma darker brown; male hypopygium with the tergite produced into two conspicuous earlike lobes that are directed beneath into the straight tergal spines; basistyle without lobes; dististyle terminal, the outer spine of outer style reduced; aedeagus beyond the enlarged base more or less bifid.

Male: Length about 6.5 mm.; wing 6.8 mm.

Rostrum and palpi black, the former subequal in length to the remainder of head. Antennae black throughout; flagellar segments oval, with long conspicuous verticils. Head black; eyes very large, reducing the anterior vertex to a linear strip.

Pronotum brown, the pretergites more testaceous yellow. Mesonotal praescutum and scutal lobes brown, the humeral region more yellowed; median region of scutum and the scutellum brownish-yellow; postnotum light brown, the central area of mediotergite darker. Pleura and pleurotergite more reddish-brown. Halteres with stem obscure yellow, knob infuscated. Legs with coxae brownish-yellow; remainder of legs dark brown, the outer tarsal segments paling to light brown or yellowish-brown, not whitened as in most allied species. Wings (Text-fig. 12) with a strong brownish tinge, the prearcular field more whitened; stigma elongate-oval, darker brown; veins dark brown. Venation: Branches of *Rs* gradually divergent, cell $R_2$ at margin only a trifle more extensive than cell $R_3$; *r-m* short but present; *m-cu* at near two-thirds the length of vein $M_{3+4}$ and opposite *r-m*.

Abdomen, including hypopygium, brownish black. Male hypopygium (Text-fig. 15) with the tergite, *9t*, produced into two conspicuous triangular earlike lobes that are further armed beneath with the usual lateral tergal arms, the spine of the latter straight to gently sinuous, its tip acute; entire posterior border of tergite, including the lobes, glabrous. Basistyle, *b*, unarmed with lobes but with a small concentration of setae on mesal face near proximal end. Dististyles, *d*, terminal, the outer style small, glabrous, its outer spine reduced to a triangular tubercle, the axial spine strong, decurved; inner dististyle longer, slightly dilated on basal half and here provided with scattered tubercles, each bearing a small seta. Aedeagus, *a*, beyond the enlarged base more or less bifid, curved into a circle, the tip pale.

Holotype, ♂, Rancho Grande, July 31, 1946 (Beebe-Fleming).

The yellowish-brown tarsi are quite different from those of the various species that center around *Helius* (*Helius*) *albitarsis* (Osten Sacken), which have the tarsi snowy white. The structure of the male hypopygium of the present fly is distinctive.

42. **Helius (Helius) rectispina** Alexander, 1947.

*Helius* (*Helius*) *rectispina* Alexander; *Bol. Ent. Venezolana*, 6: 43-44, fig. 2; 1947.

Rancho Grande, August 27, 1944, collected by Lichy; type. Still known only from the type locality.

### **Protohelius** Alexander.

43. **Protohelius venezolanus,** sp. n.

General coloration of body dark brown to black; antennae unusually long, nearly one-third the length of wing; legs brownish-black, the outer tarsal segments paling to brown; wings with a strong blackish tinge, the prearcular and costal fields a trifle darker; *Sc* long, $Sc_1$ ending about opposite the fork of the long straight *Rs; m-cu* just beyond the fork of *M*.

Female: Length about 7 mm.; wing 8 mm.; antenna about 2.5 mm.

Rostrum short and inconspicuous; palpi comparatively long, black. Antennae unusually long for the female sex, as shown by the measurements, black, the pedicel a trifle brightened; flagellar segments cylindrical, becoming shorter and more slender outwardly; first segment long, nearly equal to segments two and three combined; verticils short and inconspicuous. Head black, sparsely pruinose; eyes large, the anterior vertex reduced to a narrow strip.

Pronotum reduced, hidden from above by the forward projecting praescutum; pretergites testaceous yellow. Mesonotum uniformly dark brown; setae long and conspicuous, especially on scutellum. Pleura dark brown. Halteres dark brown, the extreme base of stem brightened. Legs brownish-black, the trochanters more testaceous; outer tarsal segments paling to brown; claws (female) long and slender, simple. Wings (Text-fig. 13) with a strong blackish tinge, the pre-

arcular and costal fields a trifle darker; veins brownish-black. All veins beyond cord with abundant macrotrichia. Venation: $Sc_1$ ending about opposite fork of the long straight *Rs*, $Sc_2$ near its tip; $R_2$ and $R_{1+2}$ subequal in length, the former pale but strong; $R_{4+5}$ about four-fifths as long as *Rs;* inner end of cell 1*st* $M_2$ arcuated; *m-cu* just beyond the fork of *M*.

Abdominal tergites brown, the borders narrowly more blackened, sternites more uniformly paler brown. Ovipositor with valves very long, the cerci slender, gently upcurved.

Holotype, ♀, Rancho Grande, July 27, 1946 (Beebe-Fleming).

The only other neotropical species of the genus is *Protohelius cisatlanticus* Alexander, of Ecuador. This differs in the much paler color of the body, legs and wings and in the details of venation. From the length of the antennae in the female sex of the present fly it is suspected that this organ in the male may be considerably longer than in *cisatlanticus*. Each of the two species mentioned is known from a single specimen, *cisatlanticus* a male, *venezolanus* a female, and in these the antennae are virtually equal in both cases. Almost invariably in the Tipulidae, species having elongate antennae in the male sex have these much shorter in the corresponding females.

### Hexatomini.

### **Paradelphomyia** Alexander.

44. **Paradelphomyia (Oxyrhiza) venezolana,** sp. n.

General coloration of thorax almost uniformly medium brown; wings with a weak brownish tinge, stigma oval, pale brown; macrotrichia of wing cells very sparse, in the extreme outer ends of cells $R_3$ to $M_1$ inclusive; wings (male) widest nearly opposite the termination of vein 2*nd A;* male hypopygium with the arms of the ventral fork slender, their tips very feebly dilated, subacute; gonapophysis with the blade triangular, the mesal angle unusually slender and pointed.

Male: Length about 4 mm.; wing 4.4 mm.

Rostrum black; palpi dark brown Antennae dark brown throughout; basal flagellar segments oval, the outer ones passing into cylindrical; verticils elongate. Head above dark.

Thorax almost uniformly medium brown, the posterior sclerites somewhat more testaceous; praescutal setae very sparse but long. Halteres pale. Legs with the coxae brownish-yellow; trochanters light yellow; remainder of legs brown, the tarsal segments paling to yellowish brown; tibial spurs present. Wings (Text-fig. 14) with a weak brownish tinge, the prearcular and costal fields a trifle more yellowed; stigma oval, pale brown; scarcely apparent dark seams over cord and outer end of cell 1*st* $M_2$, best evidenced by a slight deepening in color of the veins, the remaining veins pale brown, yellowed in the brightened fields. Wings (male) conspicuously widened nearly opposite the termination of vein 2*nd A*. Macrotrichia of cells very sparse and restricted, in the extreme outer ends of cells $R_3$ to $M_1$, inclusive, most numerous in cell $R_4$ where they total 12 or 13. Venation: $Sc_1$ ending about opposite fork of *Rs*, $Sc_2$ nearly opposite two-thirds the length of this vein; veins $R_3$ and $R_4$ nearly parallel to one another, not as conspicuously divergent as in *costaricensis*, cell $R_3$ at margin narrower; *m-cu* only a little more than its own length beyond the fork of *M*.

Abdomen pale brown, the hypopygium and eighth segment brownish black. Male hypopygium (Text-fig. 18) with the outer dististyle terminating in two slightly unequal spines, the additional ventral spine unusually long and slender. Gonapophysis, *g*, with the apical blade triangular, the mesal angle unusually slender and pointed. Each arm of the ventral fork slender, the tip very feebly to scarcely dilated, the apex subacute.

Holotype, ♂, Rancho Grande, July 25, 1948 (Beebe-Fleming); migrant No. 481374.

The most similar regional species is *Paradelphomyia (Oxyrhiza) costaricensis* (Alexander), which differs in the details of venation, as described. Unfortunately, the male sex of *costaricensis* is still unknown and the important hypopygial features cannot be compared at this time. The tropical American species of the genus have been considered in a paper by the writer (*Rev. de Entomologia,* 19: 151-153, fig. 2; 1948).

### **Austrolimnophila** Alexander.

45. **Austrolimnophila (Austrolimnophila) vivas-berthieri** Alexander, 1938.

*Austrolimnophila (Austrolimnophila) vivas-berthieri* Alexander; *Rev. de Entomologia,* 9: 436-437; 1938.

Rancho Grande, September 5, 1937, Vivas-Berthier; type.

The species is still known only from the unique type.

The tropical American species of *Austrolimnophila* are discussed by the writer elsewhere (*Rev. de Entomologia,* 19: 153-168, figs. 3, 4, 7-18; 1948).

### **Epiphragma** Osten Sacken.

46. **Epiphragma (Epiphragma) enixa** Alexander, 1939.

*Epiphragma (Epiphragma) enixa* Alexander; *Ann. Mag. Nat Hist.,* (11) 3: 190-192; 1939.

Rancho Grande, March 15, May 8, 1946 (Beebe-Fleming). The types were from Abitagua, Ecuador, 1200 meters, March 29, 1937, collected by Clark-Macintyre. The species is still known only from Ecuador and Venezuela.

47. **Epiphragma (Epiphragma) persancta** Alexander, 1938.

*Epiphragma (Epiphragma) persancta* Alexander; *Rev. de Entomologia,* 9: 248-249; 1938.

Rancho Grande, March 28, April 18, May

8-23, 1946; April 10, May 8, 1945; April 25-May 3, 1948. Part of the type material was taken here on September 5, 1947, by Vivas-Berthier. The species occurs from Venezuela to southeastern Brazil.

48. **Epiphragma (Epiphragma) solatrix** (Osten Sacken, 1859).

*Limnophila* (*Epiphragma*) *solatrix* Osten Sacken; *Proc. Acad. Nat. Sci. Philadelphia*, for 1859: 238; 1859.

Rancho Grande, July 18-23, August 5, 1946. Also taken here August 29, 1937, by Vivas-Berthier. The species was originally described from the eastern United States. It ranges from southern New York through Mexico and Central America to northern Argentina.

The neotropical species of *Epiphragma* have been discussed by the writer (*Rev. de Entomologia*, 19: 168-175, fig. 5; 1948).

### Polymera Wiedemann.

49. **Polymera (Polymerodes) conjunctoides** Alexander, 1920.

*Polymera* (*Polymerodes*) *conjunctoides* Alexander; *Ent. News*, 31: 74-75; 1920.

Rancho Grande, June 28, 1946; 2 ♂♂. The type was from Itacoatiara, Amazonian Brazil, October 16, 1919, collected by Parish. New to Venezuela; formerly from Amazonian Brazil, Ecuador and Peru.

The neotropical species of *Polymera* are considered in a paper by the writer (*Rev. de Entomologia*, 19: 182-190, figs 27-33; 1948).

### Limnophila Macquart.

50. **Limnophila guttulatissima** Alexander, 1913.

*Limnophila guttulatissima* Alexander; *Proc. U. S. Nat. Mus.*, 44: 546-547, fig. 38; 1913.

Rancho Grande, July 17, 1946. Type from Totonicapan, Guatemala, collected by Eisen. Known hitherto from Guatemala and Costa Rica.

The neotropical species of *Limnophila* are discussed in a paper by the writer (*Rev. de Entomologia*, 19: 513-518, figs. 6, 7; 1948).

### Shannonomyia Alexander.

51. **Shannonomyia araguae** Alexander, 1947.

*Shannonomyia araguae* Alexander; *Bol. Ent. Venezolana*, 6: 48-50, figs. 3-4; 1947.

Rancho Grande, July 25, 1948 (Beebe-Fleming); migrant No. 481374. The type was taken at this station on August 24, 1944, by Lichy. Still known only from the type locality.

52. **Shannonomyia lathraea** (Alexander, 1926).

*Pilaria lathraea* Alexander; *Ann. Ent. Soc. America*, 19: 386-387; 1926.

Rancho Grande, May 9, 1948; a broken ♂, taken over a pool of water by a steep mossy rock cliff. Type from San Lorenzo Mt., Colombia, taken December 13, 1922. Known hitherto only from Colombia.

53. **Shannonomyia providens**, sp. n.

Mesonotal praescutum light brown with three darker stripes, the median one more evident; antennae short, dark brown; femora and tibia obscure yellow, the tips weakly infuscated; wings with a weak brown tinge, restrictedly patterned with darker; vein $R_2$ a short distance before fork of $R_{3+4}$; male hypopygium with the tergal lobes truncate, separated by a broad U-shaped notch; outer dististyle and gonapophysis bidentate.

Male: Length about 4.5-5 mm.; wings 4.8-5.5 mm.; antenna about 0.9-1 mm.

Female: Length about 5.5 mm.; wing 6.2 mm.

Rostrum dark brown, gray pruinose; palpi black. Antennae short, dark brown; flagellar segments oval, shorter than the verticils. Head gray, somewhat clearer gray on front; a narrow blackish central line on posterior vertex; anterior vertex about two and one-half times the diameter of scape.

Pronotum gray. Mesonotal praescutum light brown, the surface pruinose; three fairly evident brown stripes, the lateral pair less distinct, crossing the suture onto the scutal lobes; posterior sclerites of notum brownish-gray. Pleurotergite and dorsal part of pleura brownish-gray, the ventral pleurites and sternum light yellow. Halteres dusky, the large knobs still more darkened. Legs with the coxae and trochanters pale yellow, the fore coxae a trifle more darkened; femora and tibiae obscure yellow, the tips weakly infuscated; tarsi brownish-yellow, the terminal segments darker. Wings (Text-fig. 19) with a weak brownish tinge, the prearcular and costal fields more yellowed; a restricted darker brown pattern, including the small oval stigma and vague seams over the cord, outer end of cell *1st* $M_2$ and origin of *Rs*, best indicated by a slight deepening in color of the veins. Venation: *Sc* moderately long, $Sc_1$ ending about opposite three-fourths to four-fifths *Rs*, $Sc_2$ a short distance from its tip; *Rs* relatively long, about one-third longer than $R_{2+3+4}$; vein $R_2$ a short distance before fork of $R_{3+4}$; vein $R_4$ long, approximately three times $R_3$; cell *1st* $M_2$ a little longer than vein $M_4$; *m-cu* shortly beyond the fork of *M*.

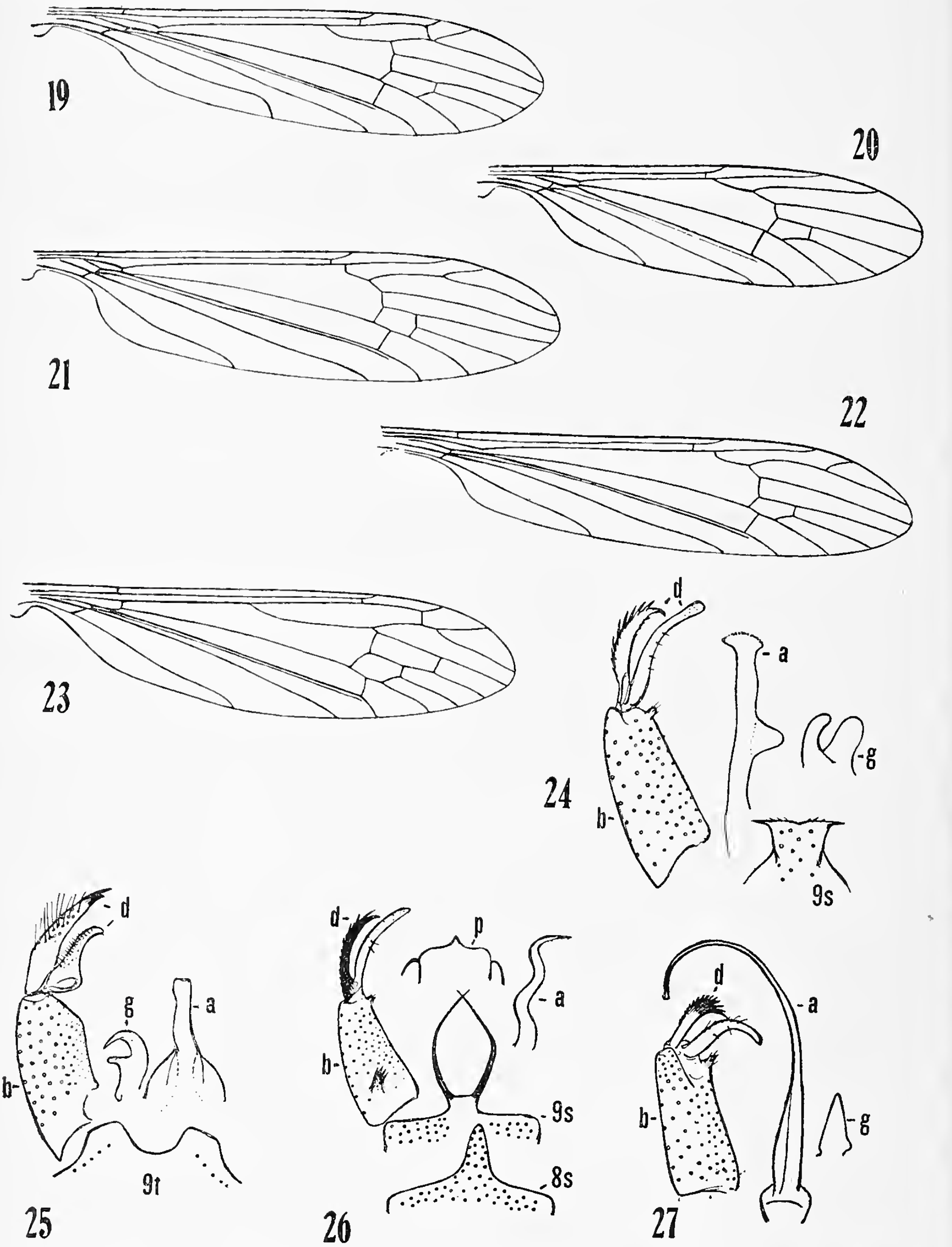
Abdominal tergites brown, with a darker brown subterminal ring involving segments six and seven, segments eight and nine more yellowed, the styli dark; basal sternites yellow. Male hypopygium (Text-fig. 25) with the tergal lobes, *9t*, truncated, separated by a broad U-shaped notch. Outer dististyle, *d*, unequally bidentate at apex, the tip blackened; outer surface of style with long setae. Inner dististyle shorter, the outer surface with abundant erect setae. Gonapophysis, *g*, bidentate, the outer spine longest.

Holotype, ♂, Rancho Grande, June 17, 1946

(Beebe-Fleming). Allotopotype, ♀, July 22, 1948; migrant No. 481365, in copula with a paratype. Paratopotypes, 1 broken ♂, with allotype; 1 ♂, July 17, 1948.

The present fly is most similar in its general appearance to species such as *Shannonomyia adumbrata* Alexander and *S. protuberans* Alexander, differing in the coloration of the body and wings and in the structure of the antennae and the male hypopygium.

The tropical American species of *Shannonomyia* have been recorded in a paper by the writer (*Rev. de Entomologia*, 19: 518-523, figs. 8, 9, 11-13; 1948).




Text-figs. 19-27. (Symbols: *a*, aedeagus; *b*, basistyle; *d*, dististyles; *g*, gonapophysis; *s*, sternite; *t*, tergite). 19—*Shannonomyia providens*, sp. n.; venation. 20—*Atarba* (*Atarba*) *quasimodo*, sp. n.; venation. 21—*Atarba* (*Ischnothrix*) *brevisector* Alexander; venation. 22—*Atarba* (*Ischnothrix*) *spinituber*, sp. n.; venation. 23—*Hexatoma* (*Eriocera*) *beebeana*, sp. n.; venation. 24—*Atarba* (*Atarba*) *quasimodo*, sp. n.; male hypopygium. 25—*Shannonomyia providens*, sp. n.; male hypopygium. 26—*Atarba* (*Ischnothrix*) *spinituber*, sp. n.; male hypopygium. 27—*Atarba* (*Atarba*) *cincticornis thamia*, subsp. n.; male hypopygium.

### ***Hexatoma*** Latreille.

54. ***Hexatoma (Eriocera) beebeana***, sp. n.

Size relatively small (wing, male, 9 mm.); general coloration black, the praescutum and scutal lobes with metallic blue reflections; fore and middle femora with about the basal third yellow, the remainder blackened, enclosing a narrow obscure yellow subterminal ring; posterior femora clear yellow basally, the tip conspicuously blackened; wings with the restricted ground whitened, much restricted by broad brown seams to the veins; cell $R_3$ unusually short, vein $R_2$ before the cell subequal in length to vein $R_{3+4}$; a supernumerary crossvein at near midlength of cell $R_5$; *m-cu* close to midlength of cell *1st* $M_2$.

Male: Length about 10 mm.; wing 9 mm.; antenna about 2.5 mm.

Rostrum brownish-black, yellow pollinose; palpi black, the first segment paler. Antennae (male) short, 7-segmented; scape and pedicel dark brown, flagellum black; first flagellar segment exceeding the combined second and third segments and a little shorter than the fourth; fourth segment nearly three times as long as the fifth. Head dark brown, sparsely pollinose on genae; vertical tubercle orange, deeply split medially.

Pronotal scutum and pleura heavily light gray pruinose, the scutellum brownish-black. Mesonotal praescutum and the scutal lobes black with distinct metallic blue reflections; remainder of notum intensely black, very sparsely pollinose, the pleurotergite more heavily so; praescutal vestiture very short and sparse. Pleura black, sparsely gray pruinose, more heavily so on the pteropleurite; dorsopleural membrane brownish-black. Halteres black. Legs with the coxae black, heavily gray pruinose; trochanters black; fore and middle femora with about the basal third yellow, the remainder blackened, enclosing a narrow and inconspicuous obscure yellow subterminal ring; tibiae brown, the tip and the tarsi more blackened; posterior femora clear yellow basally, the tip conspicuously blackened, with vague indications of a broad brownish-yellow subterminal ring, the narrow area before the apex clearer yellow; tibiae and tarsi black. Wings (Text-fig. 23) with the ground whitened, much restricted by broad brown seams to the veins; costal border and bases of cells *R* and *M*, together with the apex, more extensively and uninterruptedly brown; both Anal cells uniformly paler brown; veins brown, arculus conspicuously light yellow. Outer radial veins with abundant macrotrichia, these greatly reduced in number to virtually lacking in the medial field. Venation: $Sc_1$ ending about opposite the fork of *Rs;* vein $R_{3+4}$ subequal to vein $R_2$, both a little shorter than $R_{1+2}$, cell $R_3$ thus unusually short; a supernumerary crossvein at near midlength of cell $R_5$; *m-cu* close to midlength of cell *1st* $M_2$.

Abdominal tergites black, basal sternites medium brown, the outer ones intensely blackened; hypopygium small, obscure brownish-yellow.

Holotype, ♂, Rancho Grande, March 26, 1945 (Beebe-Fleming).

This striking crane-fly is respectfully dedicated to Dr. William Beebe. There are no very close allies so far made known and the fly will be readily recognized. The presence of supernumerary crossveins in the wings is very uncommon in species of *Eriocera*, in the neotropical fauna including only *Hexatoma (Eriocera) acunai* Alexander, of Cuba, among the described species. This latter fly has the cross-vein in cell $R_4$ instead of in cell $R_5$, as in the present species.

55. ***Hexatoma (Eriocera) bifurcata*** Alexander, 1947.

*Hexatoma (Eriocera) bifurcata* Alexander; *Bol. Ent. Venezolana*, 6: 97-99; 1947.

Rancho Grande, July 10, 1945, ♀; May 6, 1946, ♀; July 9, 1946, ♂. The type was from Choroni, Km. 25, taken September 12, 1945, by Lichy. Still known only from the state of Aragua, Venezuela.

56. ***Hexatoma (Eriocera) candidipes*** (Alexander, 1923).

*Penthoptera candidipes* Alexander; *Ent. News*, 34: 20; 1923.

Rancho Grande, July 18, 1946. Type from Tachira, Venezuela, taken April 9, 1920, by the Williamsons and Ditzler. Still known only from Venezuela.

The tropical American species of *Hexatoma (Eriocera)* have been discussed by the writer in another paper (*Rev. de Entomologia*, 19: 528-535, figs. 16-20; 1948.

### ***Atarba*** Osten Sacken.

57. ***Atarba (Ischnothrix) spinituber***, sp. n.

Color variable, the mesonotum ranging from reddish-brown to dark brown; antennae (male) elongate, exceeding the wing in length, the segments with unusually long erect setae scattered over their whole length; wings with a weak brownish tinge; *Sc* short; *Rs* short, weakly angulated; vein $R_3$ short, arcuated, less than one-third the petiole of cell $R_3$; male hypopygium with the appendage of the eighth sternite an elongate lobe, of the ninth sternite a conspicuous lyriform structure; basistyle on mesal face near proximal end with a cylindrical lobe bearing spinous setae; aedeagus sinuous to the acute apex.

Male: Length about 5.5-5.7 mm.; wing 6-6.2 mm.; antenna about 6-7 mm.

Rostrum yellow pollinose; palpi brownish-yellow. Antennae (male) elongate, exceeding the wing in length, pale brown; flagellar segments very elongate-cylindrical, with dense erect pale setae, these unusually long and conspicuous, the longest approximately two-thirds the length of the segment; in addition to the longest vestiture there is an even more abundant shorter type of seta that is about one-fourth the segment. Head dark brownish gray.

Thorax of type dark reddish-brown to brown, of the paratype much darker brown

to brownish-black. Pleura of type light yellow, of the paratype more brownish-yellow, sparsely pruinose. Halteres infuscated, the base of stem narrowly pale yellow. Legs with the coxae and trochanters yellow; remainder of legs yellowish-brown (type) to brownish-black (paratype). Wings (Text-fig. 22) with a weak brownish tinge, the oval stigma darker brown, inconspicuous; veins brown, those near wing base a trifle brighter. Venation: *Sc* short, $Sc_1$ ending just beyond origin of *Rs*, $Sc_2$ before this origin; *Rs* short, weakly angulated at origin; vein $R_3$ short, arcuated, less than one-third the petiole of cell $R_3$; cell $R_2$ at margin about one-third to two-fifths the extent of cell $R_3$; *m-cu* at near one-third the length of cell 1*st* $M_2$.

Abdomen yellowish-brown to brown, the subterminal segments still darker to form a ring; hypopygium and sternites more yellowed. Male hypopygium (Text-fig. 26) with the appendage of the eighth sternite, 8*s*, a depressed-flattened elongate lobe, narrowed to obtuse tip, with setae over the whole surface. Appendage of ninth sternite, 9*s*, profoundly lyriform, the branches unusually long and slender, near apex with weak retrorse points or roughenings. Basistyle, *b*, on mesal face of proximal half with a fingerlike lobe that is tufted with strong black spinous setae, those at apex even stouter. Outer dististyle, *d*, a slender blackened gently curved rod, provided with scattered spines along the outer face, the terminal one subequal to the apex and slightly more slender. Inner dististyle subequal in length but extending beyond the dorsal dististyle due to its place of insertion, gently arcuated. Aedeagus, *a*, sinuous to the acute apex.

Holotype, ♂, Rancho Grande, May 5, 1945 (Beebe-Fleming). Paratopotypes, ♂♂, May 7, 1945, May 27, 1948.

The closest relative of the present fly is *Atarba* (*Ischnothrix*) *brevisector* (Alexander), described from the cloud forest zone of the Silla de Caracas, 1900 meters. This is a larger fly (wing, ♀, nearly 8 mm.) that is still known only from the female sex. Besides the large size, this species has the antennal flagellum black, with short vestiture, the latter undoubtedly a sexual character. The venational details (Text-fig. 21) are distinct, particularly the outer radial field where vein $R_3$ is normally oblique and relatively long, exceeding one-half the length of the petiole of cell $R_3$; cell $R_2$ at margin scarcely one-third that of cell $R_3$.

The tropical American species of *Atarba* have been considered by the writer in another paper (*Rev. de Entomologia*, 19: 536-552, figs. 21-35; 1948).

58. ***Atarba* (*Atarba*) *cincticornis thamia*,** subsp. n.

Male: Length about 5 mm.; wing 5.5 mm.; antenna about 4.5 mm.

Antennal flagellum almost uniformly darkened, only the incisures of the more proximal segments restrictedly yellow; on outer segments the amount of pale color is somewhat increased; basal flagellar segments long-cylindrical, with conspicuous outspreading verticils and erect setae; outer segments progressively much shorter, the outer four or five scarcely more than four times as long as the diameter across base. In typical *cincticornis*, the antennae are longer, the segments more evidently bicolored, their bases distinctly thicker than their tips.

Mesonotum almost uniformly dark brown, the postnotum and pleura more pruinose. Halteres infuscated. Legs yellow, the outer tarsal segments darker. Wings with a weak brownish tinge, the costal border more yellowed; stigma small; veins pale brown, *Sc* more yellowed. Venation: $Sc_1$ ending virtually opposite the origin of *Rs*, $Sc_2$ a short distance from its tip; $Sc_1$ nearly as long as the short *Rs*, the latter subequal to the basal section of $R_5$; cell 1*st* $M_2$ nearly rectangular in outline, the second section of $M_{1+2}$ approximately twice the basal section; *m-cu* about one-third its length beyond the fork of *M*. In typical *cincticornis*, *Rs* is longer; cell 1*st* $M_2$ very small and short, the second section of vein $M_{1+2}$ being subequal to or actually shorter than the basal section; *m-cu* at or close to the fork of *M*.

Abdomen brown, with a dark brown subterminal ring; hypopygium yellow. Male hypopygium (Text-fig. 27) generally as in the typical race, particularly as regards the outer dististyle and the aedeagus. Outer dististyle, *d*, dilated on outer half, the outer margin with conspicuous black spines, those at near midlength of the group more crowded and in double rows. Inner dististyle with conspicuous setae, especially along the outer margin. Gonapophysis simple, appearing as an elongate blade, the top subacute. Aedeagus, *a*, very long and slender, longer than the combined basistyle and dististyles, the apex not or scarcely expanded. In typical *cincticornis*, the outer dististyle has the central spines shorter and arranged in several rows. Inner dististyle shorter, without conspicuous setae. Gonapophysis even more slender and elongate.

Holotype, ♂, Rancho Grande, June 26, 1946 (Beebe-Fleming).

The discovery of more material will probably result in elevating the present fly to full specific rank. Typical *cincticornis* Alexander is known from British Guiana and Ecuador.

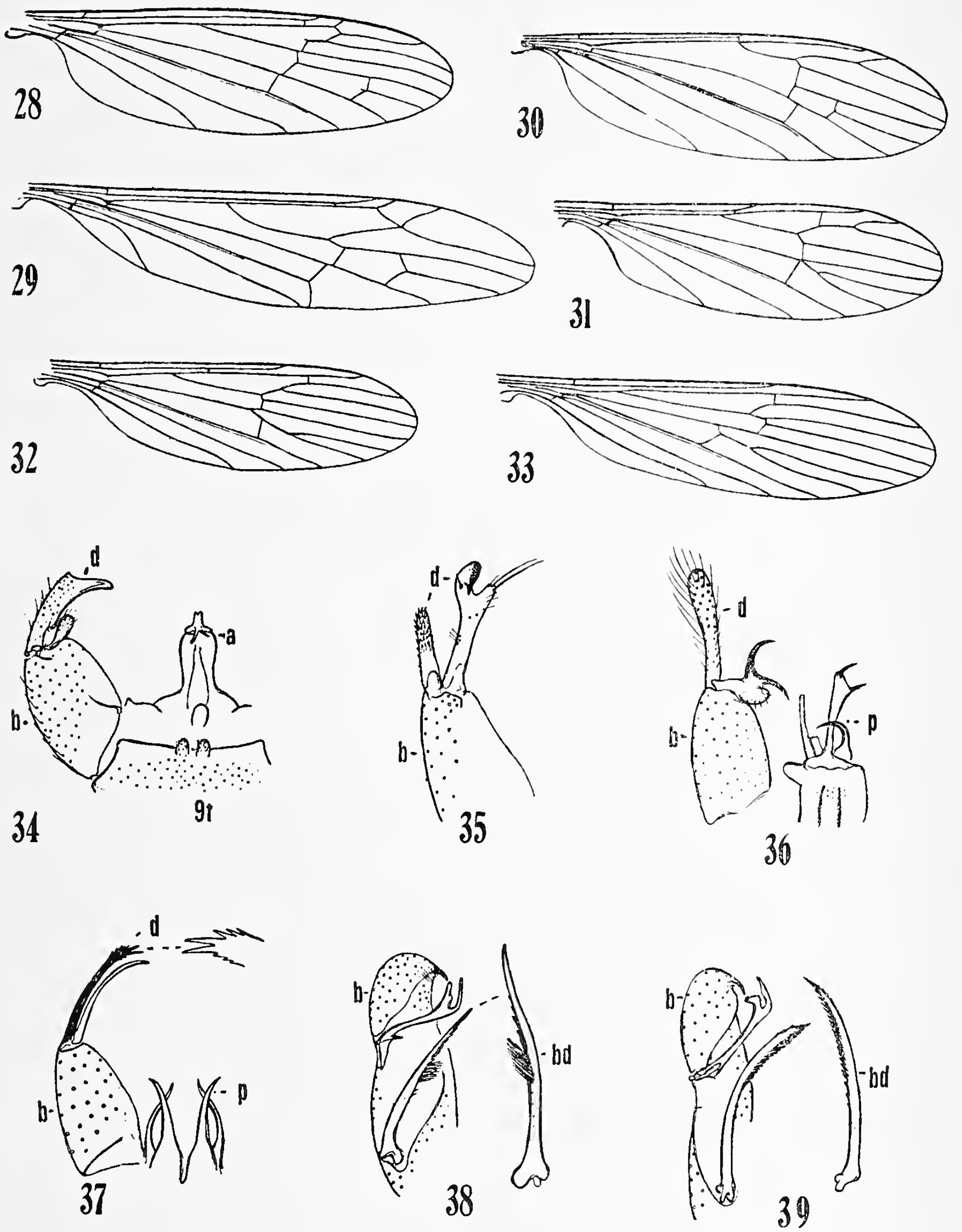
59. ***Atarba* (*Atarba*) *quasimodo*,** sp. n.

Thorax almost uniformly brownish-yellow, unpatterned; antennae (male) about one-third the length of wing, flagellum black; legs yellow; wings with a strong yellow tinge, stigma very pale brown, inconspicuous; $Sc_1$ ending about opposite one-third the length of *Rs*; cell 1*st* $M_2$ pentagonal in outline; male hypopygium with the outer lateral angles of the appendage of the ninth sternite produced into very slender spines; outer dististyle with about nine spines on outer margin; gonapophyses appearing as bilobed smooth blades; aedeagus elongate, stout, the

apex a little dilated, on margin at near midlength with a very conspicuous obtuse tubercle or hump.

Male: Length about 5 mm.; wing 4.5-4.6 mm.; antenna about 1.4-1.5 mm.

Rostrum dark brown; palpi more reddish-brown. Antennae (male) of moderate length, about one-third the length of the wing; flagellar segments long-subcylindrical, exceeding the verticils, the latter stout, about four per segment; the entire segment with a dense erect pale pubescence, these approximately one-half the length of the verticils. Head dark gray; anterior vertex broad.




TEXT-FIGS. 28-39. (Symbols: *a*, aedeagus; *b*, basistyle; *bd*, basal dististyle; *d*, dististyle; *p*, phallosome; *t*, tergite). 28—*Sigmatomera beebei*, sp. n.; venation. 29—*Trentepohlia* (*Paramongoma*) *fuscolimbata*, sp. n.; venation. 30—*Gonomyia* (*Gonomyia*) *spiculistyla*, sp. n.; venation. 31—*Erioptera* (*Empeda*) *abitaguae* Alexander; venation. 32—*Erioptera* (*Erioptera*) *beebeana*, sp. n.; venation. 33—*Molophilus* (*Molophilus*) *compactus*, sp. n.; venation. 34—*Sigmatomera beebei*, sp. n.; male hypopygium. 35—*Gonomyia* (*Gonomyia*) *spiculistyla*, sp. n.; male hypopygium. 36—*Gonomyia* (*Lipophleps*) *vindex* Alexander; male hypopygium. 37—*Erioptera* (*Erioptera*) *beebeana*, sp. n.; male hypopygium. 38—*Molophilus* (*Molophilus*) *compactus*, sp. n.; male hypopygium. 39—*Molophilus* (*Molophilus*) *flemingi*, sp. n.; male hypopygium.

Thorax almost uniformly brownish-yellow, unpatterned, the pleura more yellowed. Halteres with stem yellow, knobs weakly darkened. Legs with the coxae and trochanters reddish-yellow; remainder of legs yellow, the terminal tarsal segments more infuscated. Wings (Text-fig. 20) with a strong yellow tinge, the prearcular and costal fields clearer yellow; stigma oval, very pale brown, inconspicuous; veins yellow. Venation: *Sc* moderately long, $Sc_1$ ending about opposite one-third the length of *Rs*, $Sc_2$ faint, a short distance before this origin; branches of *Rs* very gently divergent; cell 1*st* $M_2$ pentagonal, less than one-half the basal section of $M_3$; *m-cu* variable in position, from a short distance before the fork of *M*, as illustrated, to a little beyond this fork.

Abdomen light brown, the bases of the segments paler; subterminal segments dark brown to produce a conspicuous ring; hypopygium yellow. Male hypopygium (Text-fig. 24) with the appendage of the ninth sternite, 9*s*, short and broad, the caudal margin nearly truncate, very slightly emarginate at the midline; outer lateral angles produced laterad into unusually slender spines; surface of appendage with relatively few coarse setae. Outer dististyle, *d*, relatively slender, the outer margin with teeth over virtually the whole length, totalling nine or ten, the more basal ones smaller and appressed, the outer spines longer and more conspicuous; terminal spine subequal to the subterminal one and slightly more curved; on ventral margin before apex with three or four delicate spinules. Inner dististyle a little longer than the outer style, appearing as a darkened slender rod, gently curved, the obtuse tip a little enlarged. Gonapophysis, *g*, appearing as bilobed smooth blades. Aedeagus, *a*, elongate, stout, the apex a little dilated and flaring; on margin at near midlength with a very conspicuous obtuse dilation or tubercle.

Holotype, ♂, Rancho Grande, May 12, 1945 (Beebe-Fleming). Paratopotype, ♂, pinned with type.

The present fly is quite distinct in the structure of the male hypopygium. In the prominent tubercle on the aedeagus, it suggests *Atarba* (*Atarba*) *tuberculifera* Alexander, but is an entirely different fly, being one of the smallest members of the genus whereas *tuberculifera* is one of the largest.

### ***Elephantomyia*** Osten Sacken.

60. ***Elephantomyia (Elephantomyia) setulistyla*** Alexander, 1938.

*Elephantomyia* (*Elephantomyia*) *setulistyla* Alexander; *Ann. Mag. Nat. Hist.*, (11) 1: 351-352; 1938.

Rancho Grande, May 12-July 8, 1946; July 17, 1948. The type was from Abitagua, Ecuador, 1200 meters, April 7, 1937, collected by Clarke-Macintyre. Known only from Ecuador and Venezuela.

The tropical American species of *Elephantomyia* have been listed in a further paper by the writer (*Rev. de Entomologia*, 19: 552-556, figs. 27, 28, 36; 1948).

## ERIOPTERINI.

### ***Sigmatomera*** Osten Sacken.

61. ***Sigmatomera beebei***, sp. n.

General coloration reddish-yellow, unpatterned; halteres and legs yellow; wings uniformly rich yellow, all the veins deep yellow; cell 1*st* $M_2$ elongate, subequal in length to the distal section of vein $M_{1+2}$; male hypopygium with the dorsal lobules of the ninth tergite very small, suboval in outline; inner dististyle stout, the lobe on its outer margin very low and obtuse; aedeagus without elongate spines at apex.

Male: Length about 14 mm.; wing 14.5 mm.

Head broken. Prothorax and mesothorax almost uniformly reddish-yellow, the praescutum with three such stripes on a slightly more yellowed ground. Halteres uniformly yellow. Legs yellow, only the terminal tarsal segment brown. Wings (Text-fig. 28) uniformly rich yellow, the prearcular and costal borders more saturated yellow; all veins deep yellow. Venation: $Sc_1$ ending about opposite one-third the length of the outer or angulated section of $R_{2+3+4}$, $Sc_2$ opposite this angulation; $R_{2+3+4}$ angulated just before midlength, with a long spur jutting basad into cell $R_1$ at the angle; cell 1*st* $M_2$ elongate, widened outwardly, subequal in length to the distal section of vein $M_{1+2}$; basal section of vein $M_3$, with a weak spur jutting basad into cell 1*st* $M_2$; *m-cu* at or close to the fork of *M*.

Abdomen brownish-yellow, hypopygium yellow. Male hypopygium (Text-fig. 34) with the dorsal lobules of the ninth tergite, 9*t*, very small, suboval in outline, separated by a space that is subequal to the diameter of either lobe. Inner dististyle stout, the lobe on outer margin very low and obtuse. Aedeagus, *a*, stout, terminating in a small central point, not produced into elongate spines, as common in the genus; if present, these latter are microscopic.

Holotype, ♂, Rancho Grande, May 2, 1945 (Beebe-Fleming).

I am very pleased to name this species for Dr. William Beebe. The fly is most similar to other species with unpatterned wings, such as *Sigmatomera flavipennis* Osten Sacken (genotype) and *S. occulta* Alexander. It differs from these and from all other known forms in the uniformly bright yellow veins and in the structure of the male hypopygium. In the latter respect, the species differs very markedly from *flavipennis*, which has the inner dististyle long and slender. The species that have this style most like that in the present fly include *S. occulta* and *S. shannoniana* Alexander, which differ evidently in the pattern of the wings and in the details of the hypopygium, including the tergite, inner dististyle and aedeagus.

The tropical American species of *Sigmatomera* have been listed in another report by

the writer (*Rev. de Entomologia,* 18: 68-69, figs. 3, 4; 1947).

### *Trentepohlia* Bigot.

62. ***Trentepohlia (Paramongoma) fuscolimbata,*** sp. n.

Mesonotum and pleura almost uniformly reddish-brown; legs medium brown, the tip of the tibia and the tarsi paling to cream-yellow; wings grayish-subhyaline; stigma relatively large and conspicuous, subcircular to short-oval in outline; veins of the proximal three-fourths of wing extensively seamed with paler brown; vein $R_3$ oblique.

Female: Length about 10 mm.; wing 8.2 mm.

Rostrum yellow. Antennae with the scape and pedicel dark brown; flagellum broken. Head brown; anterior vertex reduced to a linear strip that is subequal in width to a single row of ommatidia.

Cervical region dark brown above, paler on sides. Pronotum dark brown above, paling to yellowish-brown laterally. Mesonotum and pleura almost uniformly reddish-brown, the scutellum and especially the postnotum sparsely gray pruinose. Halteres pale. Legs with the coxae reddish-brown; trochanters yellow; legs medium brown, the genua, especially the tibial base, very narrowly and almost insensibly whitened; tip of tibia and the tarsi paling to cream-yellow. Wings (Text-fig. 29) grayish-subhyaline; stigma relatively large and conspicuous, subcircular to short-oval; veins before level of outer end of cell *1st* $M_2$ extensively seamed with paler brown, such cloudings on *Rs*, $R_{2+3+4}$, cord, outer end of cell *1st* $M_2$, outer end of *M* and $M_{3+4}$, distal half of *Cu,* and at and near the bases of the Anal cells; wing tip even more vaguely suffused; veins brownish-yellow, somewhat clearer yellow in the outer costal field. Venation: Vein $R_3$ more oblique than in *suffuscipes*; cell *1st* $M_2$ broader; *m-cu* only a short distance before the fork of *M*.

Abdominal tergites dark brown, sternites yellow; genital shield brownish-yellow. Cerci relatively long and very slender.

Holotype, ♀, Rancho Grande, May 11, 1945 (Beebe-Fleming).

The most similar regional species is *Trentepohlia (Paramongoma) suffuscipes* Alexander, which differs in the coloration of the body, legs and wings, as well as in slight details of the venation.

The tropical American species of *Trentepohlia* have been considered earlier by the writer (*Rev. de Entomologia,* 18: 69-72, figs. 5-7; 1947).

### *Teucholabis* Osten Sacken.

63. ***Teucholabis (Teucholabis) anthracina*** Alexander, 1921.

*Teucholabis anthracina* Alexander; *Proc. Acad. Nat. Sci. Philadelphia,* for 1921: 85-86; 1921.

Rancho Grande, May 12, 1945; 1 ♀ only. The type was from the Napo River, Amazonian Peru, taken June 14, 1920, by Parish. The fly was known hitherto from Ecuador and Peru. Despite the lack of the male sex I can see no reason to question the determination.

The tropical American species of *Teucholabis* were discussed by the writer in an earlier report (*Rev. de Entomologia,* 17: 375-400, figs. 1-14; 1946).

### *Gnophomyia* Osten Sacken.

64. ***Gnophomyia (Gnophomyia) digitiformis*** Alexander, 1941.

*Gnophomyia (Gnophomyia) digitiformis* Alexander; *Journ. N. Y. Ent. Soc.,* 49: 144-145; 1941.

Rancho Grande, March 27; April 8-24; June 18; July 1-18; August 16, 1946. Type from San Esteban, Venezuela, taken December 19, 1939, by Anduze. The species is still known only from Venezuela.

The neotropical species of *Gnophomyia* have been discussed briefly in another paper by the writer (*Rev. de Entomologia,* 18: 72-80, figs. 8-12; 1947).

### *Neognophomyia* Alexander.

65. ***Neognophomyia monophora*** Alexander, 1941.

*Neognophomyia monophora* Alexander; *Journ. N. Y. Ent. Soc.,* 49: 146-147; 1941.

Rancho Grande, April 24, 1948 (No. 4872); July 25, 1948 (No. 481374), migrant series. The types were from San Esteban, Venezuela, December 28, 1939, Anduze, and Borburata, Venezuela, 500 meters, March 10-15, 1940, Anduze. Still known only from Venezuela.

The tropical American species of *Neognophomyia* are listed by the writer (*Rev. de Entomologia,* 18: 81-82, fig. 16; 1947).

### *Gonomyia* Meigen.

66. ***Gonomyia (Gonomyia) spiculistyla,*** sp. n.

Mesonotum chiefly medium brown; scutellum obscure yellow; legs brownish-black; wings with a weak dusky tinge; $Sc_1$ ending opposite origin of *Rs*, $R_{2+3+4}$ subequal to *Rs*; male hypopygium with the outer dististyle a simple stout rod, the surface with abundant short spines or spicules, without setae.

Male: Length about 4 mm.; wing 4.2 mm.

Head broken. Pronotum brown, the pretergites light yellow. Mesonotum chiefly medium brown, the praescutum darker medially; scutal lobes dark brown; median region of scutum and the scutellum obscure yellow, the latter restrictedly darkened at base; postnotum brownish-gray, the lateral borders of the mediotergite yellow; pleurotergite paler and pruinose. Pleura variegated dark reddish-brown and yellow, the latter color producing a vague stripe on the dorsal sternopleurite and pteropleurite. Halteres

dark brown. Legs with the coxae dark reddish-brown; trochanters yellow; remainder of legs brownish-black. Wings (Text-fig. 30) with a weak dusky tinge, the stigmal area slightly darker, ill-delimited and vague; veins dark brown. Venation: $Sc_1$ ending opposite origin of *Rs*, $Sc_2$ at its tip; $R_{2+3+4}$ subequal to or a trifle longer than *Rs*; vein $R_3$ oblique; *r-m* long, subequal to *m-cu*, the latter at near one-third the length of cell 1st $M_2$.

Abdomen dark brown. Male hypopygium with the dististyles (Text-fig. 35, *d*) distinctive; outer style a simple stout rod, its surface densely covered with short spines or triangular points to produce a spiculose appearance, without setae. Inner dististyle appearing as a straight rod, before apex on outer margin with a strong arm that terminates in a flattened black plate, strongly recurved, its lower apical angle further produced into a point; main axis of style bearing the usual two strong fasciculate setae, additional to a few other normal bristles. Phallosome broken and in part lost before mounting; a single strong slender spine persists in the slide mount; from a cursory preliminary examination made before the loss of this part, it is believed that there was a second spine and a further elongate pale rod that was expanded at its apex into a triangular blade, the apex shallowly emarginate.

Holotype, ♂, Rancho Grande, July 10, 1946 (Beebe-Fleming).

While similar in its general appearance to species such as *Gonomyia* (*Gonomyia*) *juarezi* Alexander, *G.* (*G.*) *methodica* Alexander, and others, the present fly is entirely distinct in the structure of the male hypopygium, including both the dististyles and the phallosome.

67. **Gonomyia (Lipophleps) vindex** Alexander, 1941.

*Gonomyia* (*Lipophleps*) *vindex* Alexander; *Journ. N. Y. Ent. Soc.*, 49: 142-143; 1941.

Rancho Grande, May 12, 1945. The type was from Borburata, Venezuela, 500 meters, taken March 15, 1940, by Anduze. Still known only from Venezuela. In the present specimen, the male hypopygium (Text-fig. 36), while being generally similar to that of the type, differs in slight details, especially the longest element of the phallosome, *p*, where the outer spine is longer and more conspicuous than in the type.

68. **Gonomyia (Paralipophleps) lemniscata** Alexander, 1931.

*Gonomyia* (*Lipophleps*) *lemniscata* Alexander; *Ann. Ent. Soc. America*, 24: 634-635; 1931.

*Gonomyia* (*Paralipophleps*) *lemniscata* Alexander; *Rev. de Entomologia*, 18: 97-98; 1947.

Rancho Grande, July 10, 1946. The types were from Vista Nieve, Mount Santa Marta, Colombia, 5,000 feet, August 8, 1926, taken by Fred W. Walker, and from Jaragua, Santa Catharina, Brazil, taken September 20, 1929. The species is known from Colombia, Venezuela and southeastern Brazil.

The tropical American species of *Gonomyia* have been discussed in a paper by the writer (*Rev. de Entomologia*, 18: 83-99, figs. 17-29; 1947).

### *Erioptera* Meigen.

69. ***Erioptera (Erioptera) beebeana***, sp. n.

Allied to *multiannulata;* general coloration of thorax and abdomen dark brown, the thoracic pleura with a longitudinal silvery white stripe; femora with three dark brown and three china-white rings; tibiae and basitarsi variegated with darkened annuli; wings with a strong light brown tinge, unpatterned; male hypopygium with both dististyles slender, the outer one terminating in several strong spines; inner styles very slender; phallosome with the apophyses bispinous.

Male: Length about 2.5 mm.; wing 3 mm.

Rostrum brown; palpi black. Antennae black throughout; flagellar segments oval, with very long verticils. Head above gray.

Pronotum and mesonotum almost uniformly dark brown, the surface with a very sparse pruinosity; praescutum with two very faintly indicated darker brown stripes; anterior pretergites obscure whitish, the region before the wing root pale. Pleura and pleurotergite dark brown, pruinose, with a narrow silvery white longitudinal stripe that is bordered both above and below by a slightly narrower more blackened line. Halteres clear light yellow. Legs with the fore coxae dark brown, the middle pair a little paler; posterior coxae and trochanters testaceous yellow; femora conspicuously ringed with dark brown and china white, there being three dark rings and three narrower white ones, the last terminal; tibiae yellow with a narrow nearly basal dark ring and a more extensive subterminal one, the latter a little less than the pale tip; tarsi yellow, the proximal end of the basitarsi narrowly darkened; two outer tarsal segments infuscated; vestiture of legs including setae and normal linear scales. Wings (Text-fig. 32) with a strong light brown tinge, the prearcular and costal regions a trifle more brightened; veins brownish-yellow, the vestiture pale brown. Venation: Petiole of cell $M_3$ from one-third to one-half longer than *m-cu*; vein *2nd A* gently sinuous on nearly the outer half.

Abdomen, including hypopygium, dark brown, the ninth segment more yellowed. Male hypopygium (Text-fig. 37) with both dististyles, *d*, slender, terminal in position; outer style blackened, at apex with about three strong spines, with other smaller denticles back from tip, inner style subequal in length but even more slender, glabrous, the tip acute, near apex with two or three pale punctures. Phallosome, *p*, with powerful horn-colored spinous apophyses, one pair on either side, the strong inner spines nearly

parallel to one another, their tips gently outcurved, acute; lateral arms approximately equal in length but a little more slender and sinuous.

Holotype, ♂, Rancho Grande, July 25, 1948 (Beebe-Fleming); migrant series.

This attractive crane-fly is named in honor of Dr. William Beebe. The most similar regional species include *Erioptera* (*Erioptera*) *multiannulata* Alexander, *E.* (*E.*) *polydonta* Alexander, and *E.* (*E.*) *polytricha* Alexander, all of which have the male hypopygium entirely distinct in structure.

The neotropical species of *Erioptera* have been considered in an earlier report by the writer (*Rev. de Entomologia*, 18: 328-337, figs. 10-17; 1947).

70. ***Erioptera (Erioptera) celestis*** Alexander, 1940.

*Erioptera* (*Erioptera*) *celestis* Alexander; *Ann. Mag. Nat. Hist.*, (11) 5: 294-296; 1940.

Rancho Grande, July 25, 1948 (Beebe-Fleming); migrant, No. 481374. The type was from Abitagua, Ecuador, 1200 meters, taken April 5, 1937, by Clarke-Macintyre. Known only from Ecuador and Venezuela.

71. ***Erioptera (Empeda) abitaguai*** Alexander, 1941.

*Erioptera* (*Empeda*) *abitaguai* Alexander; *Ann. Mag. Nat. Hist.*, (11) 8: 131-132; 1941.

Rancho Grande, May 12, June 11-28, July 8-10, 1946.

The type was from Abitagua, Ecuador, 1100 meters, taken September 1, 1939, by Clarke-Macintyre. Known only from Ecuador and Venezuela. The wing venation is shown (Text-fig. 31).

### ***Molophilus*** Curtis.

72. ***Molophilus (Molophilus) compactus***, sp. n.

Belongs to the *plagiatus* group; mesonotum chiefly reddish-brown, unpatterned; antennae (male) relatively long, nearly one-half the length of the body; wings with a strong brownish tinge; male hypopygium with the basal dististyle a slender nearly straight rod that narrows into a long spine, the lower face at near midlength with a compact group of erect setae, beyond this brush with a few strongly appressed spinous points.

Male: Length about 3.2 mm.; wing 4 mm.; antenna about 1.5 mm.

Rostrum and palpi black. Antennae relatively long, nearly one-half the body, black throughout; flagellar segments long-subcylindrical; longest verticils unilaterally distributed, nearly twice as long as the segments; additional shorter erect pale verticils. Head gray.

Pronotum brown, darker laterally; pretergites pale yellow. Mesonotum chiefly reddish-brown, the praescutum unpatterned. Pleura darker brown. Halteres yellow basally, darker beyond, with golden yellow vestiture. Legs with the coxae and trochanters testaceous yellow; remainder of legs medium brown, the outer tarsal segments more blackened. Wings (Text-fig. 33) with a strong brownish tinge, the prearcular and costal fields slightly more yellowed; veins and macrotrichia brown. Venation; $R_2$ lying slightly distad of the level of *r-m;* petiole of cell $M_3$ about one-fourth longer than the slightly sinuous *m-cu;* vein *2nd A* long, ending about opposite midlength of *m-cu.*

Abdomen brown, the hypopygium brownish-black. Male hypopygium (Text-fig. 38) with the beak of the basistyle, *b*, slender. Outer dististyle with the two arms unequal, the more distal one slender. Basal dististyle, *bd*, a slender nearly straight rod that narrows into a long spine, on lower face at near midlength with a compact group of erect setae, beyond this brush with a few strongly appressed spinous points. Phallosomic plate unusually small, oval, the surface glabrous.

Holotype, ♂, Rancho Grande, June 28, 1946 (Beebe-Fleming).

The most similar regional species include *Molophilus* (*Molophilus*) *brownianus* Alexander, *M.* (*M.*) *capricornis* Alexander, and *M.* (*M.*) *paganus* Alexander, all differing from the present fly and among themselves chiefly in the structure of the male hypopygium, particularly of the basal dististyle.

73. ***Molophilus (Molophilus) flemingi***, sp. n.

Belongs to the *plagiatus* group; thorax almost uniformly black; antennae (male) relatively short; halteres yellow; legs black; wings grayish-subhyaline, vaguely crossbanded with pale brown, the bands lying at cord and beyond the arculus; male hypopygium with the basal dististyle a long gently curved rod that terminates in a short spine; lower face of distal half of style with a series of strong appressed spines.

Male: Length about 4 mm.; wing 4.5 mm.; antenna about 1 mm.

Rostrum and palpi black. Antenna (male) relatively short, only about one-fourth the length of body, black throughout; flagellar segments subcylindrical or long-suboval, gradually decreasing in length and diameter outwardly; verticils scattered, much exceeding the segments; remaining vestiture short and inconspicuous. Head gray.

Thorax almost uniformly black; pretergites very narrow, testaceous yellow. Halteres yellow. Legs with the coxae infuscated basally, paling to yellow outwardly; trochanters yellow; femora dark brown, yellow basally; remainder of legs black; fore tibia (male) with a linear glandular swelling. Wings grayish subhyaline, vaguely crossbanded with pale brown, including a band at cord and another across the postarcular region; prearcular field yellow; veins brown, yellow in the more brightened portions. Venation: $R_2$ in approximate transverse alignment with *r-m;* petiole of cell $M_3$ a little longer than *m-cu;* vein *2nd A* relatively short, ending slightly beyond the posterior end of *m-cu.*

Abdomen, including hypopygium, brownish-black to black. Male hypopygium (Text-fig. 39) with the beak of the basistyle, *b*, slender. Outer dististyle elongate, the two arms unequal, the inner long and slender. Basal dististyle, *bd*, a long slender gently curved rod, the terminal spine short and stout; lower face of distal half of style with a series of strong appressed spines, on proximal half more scattered and finally becoming tuberculate; outer face of style with a few small inconspicuous denticles back from apex.

Holotype, ♂, Rancho Grande, June 28, 1946 (Beebe-Fleming).

I take unusual pleasure in naming this distinct fly for Mr. Henry Fleming, Entomologist of the Department of Tropical Research of the New York Zoological Society, whose diligent collecting has added materially to our knowledge of the crane-flies of Venezuela. The fly is quite distinct from the other members of the *plagiatus* group that have the basal dististyle of the male hypopygium of somewhat the same structure and appearance. These include *Molophilus* (*Molophilus*) *brownianus* Alexander, *M.* (*M.*) *capricornis* Alexander, *M.* (*M.*) *compactus*, sp. n., *M.* (*M.*) *luxuriosus* Alexander, *M.* (*M.*) *paganus* Alexander, and some others, all differing among themselves in the pattern of the wings, length and structure of the antennae, and in the details of structure of the male hypopygium.

The tropical American species of *Molophilus* have been listed by the writer in another report (*Rev. de Entomologia*, 18: 338-353, figs. 19-28; 1947).

### **Styringomyia** Loew.

74. **Styringomyia americana** Alexander, 1914.

*Styringomyia americana* Alexander; *Trans. Amer. Ent. Soc.*, 40: 231; 1914.

Rancho Grande, July 10, 1946. The type was taken at Mallali, British Guiana, on March 8, 1913, by Parish. This is the most widely distributed of the American species of the genus, occurring in British Honduras, Costa Rica, Colombia, Venezuela, British Guiana, Surinam and Ecuador.

The tropical American species of *Styringomyia* have been discussed in an earlier paper by the writer (*Rev. de Entomologia*, 18: 354-356, fig. 29; 1947).

### **Toxorhina** Loew.

75. **Toxorhina (Toxorhina) pergracilis** Alexander, 1944.

*Toxorhina* (*Toxorhina*) *pergracilis* Alexander; *Ann. Mag. Nat. Hist.*, (11) 11: 181-182, fig. 13; 1944.

Rancho Grande, June 28, July 10-27, August 1, 1946. The type was from Ayna, La Mar, Ayacucho, Peru, 2400 meters, collected April 27, 1941, by Woytkowski. Known only from Peru and Venezuela.

76. **Toxorhina (Toxorhina) stenophallus** Alexander, 1937.

*Toxorhina* (*Toxorhina*) *stenophallus* Alexander; *Ann. Mag. Nat. Hist.*, (10) 20: 503-504; 1937.

Rancho Grande, August 27, 1944, collected by Lichy. The type was from Nova Teutonia, southeastern Brazil, taken September 30, 1935, by Plaumann. Still known only from Venezuela and Brazil.

The tropical American species of *Toxorhina* have been considered by the writer in an earlier report (*Rev. de Entomologia*, 18: 356-360, figs. 30-32; 1947).

# 3.

# Migration of Danaidae, Ithomiidae, Acraeidae and Heliconidae (Butterflies) at Rancho Grande, North-central Venezuela.[1]

WILLIAM BEEBE.

*Director, Department of Tropical Research, New York Zoological Society.*

(Text-figure 1).

[This is one of a series of papers resulting from the 45th, 46th and 47th Expeditions of the Department of Tropical Research of the New York Zoological Society, made during 1945, 1946 and 1948, under the direction of Dr. William Beebe, with headquarters at Rancho Grande in the National Park of Aragua, Venezuela. The expeditions were made possible through the generous cooperation of the National Government of Venezuela and of the Creole Petroleum Corporation.

[The characteristics of the research area are in brief as follows: Rancho Grande is located in north-central Venezuela (10° 21′ N. Lat., 67° 41′ W. Long.), 80 kilometers west of Caracas, at an elevation of 1,100 meters in the undisturbed montane rain forest which covers this part of the Caribbean range of the Andes. The migration flyway of Portachuelo Pass, which is also the water-shed between the Caribbean and Lake Valencia, is 200 meters from Rancho Grande. Adjacent ecological zones include seasonal forest, savanna, thorn woodland, cactus scrub, the fresh-water lake of Valencia and various marine littoral zones. The Rancho Grande area is generally subtropical, being uniformly cool and damp throughout the year because of the prevalence of the mountain cloud cap. The dry season extends from January into April. The average humidity during the expeditions, including parts of both wet and dry seasons, was 94.4%; the average temperature during the same period was 18° C.; the average annual rainfall over a five-year period was 174 cm. The flora is marked by an abundance of mosses, ferns and epiphytes of many kinds, as well as a few gigantic trees. For further details see Beebe and Crane, *Zoologica*, Vol. 32, No. 5, 1947. Unless otherwise stated, the specimens discussed in the present paper were taken in the montane cloud forest zone, within a radius of one kilometer of Rancho Grande.

[For an account of Portachuelo Pass, together with a general introduction to the groups of migrating insects and migrating factors, see "Insect Migration at Rancho Grande," by William Beebe, *Zoologica*, 1949, Vol. 34, No. 12, pp. 107-110].

## MIGRATION OF DANAIDAE.

Among the migrants through Portachuelo Pass are two members of the subfamily Danainae. The first is *Danaus plexippus megalippe*, so close to our northern monarch, *D. p. plexippus*, that it is impossible to distinguish them in flight. The second species is *Danaus eresimus eresimus*, corresponding to our northern queen, *Danaus gilippus berenice*.

The monarch is a notable migrant in the United States, but its neotropical subspecies has been considered, as in the case of many tropical birds, to be a permanent resident.

In the course of our Rancho Grande observations throughout the years 1945, 1946 and 1948 we recorded 643 *megalippe* passing southward through the Pass. A much larger number of *eresimus* was recorded, 5,254 altogether, but these were concentrated within a comparatively brief space of time, more than 5,000 on July 21.

### **Danaus plexippus megalippe** (Hübner).

*Field Name*: Southern Monarch.

*Species Range*: North and South America and the West Indies.

*Subspecies Range*: Northern and western South America.

*Field Characters*: Unmistakable to anyone who knows the northern monarch, *D. p. plexippus*. The chief subspecific distinction is the whiteness or the tawny appearance of the forewing spots. This is impossible to detect in flying insects. In every captured migrating specimen and in those observed close at hand, at rest, the spots were *megalippe*-white. This also agrees with the geographical locale. The only possibility of confusion (and that hardly) is with the smaller and darker *Danaus e. eresimus*.

*Number*: Total recorded, 643. Taken, 5.

*Sex*: Both sexes seen and taken.

*Date*: April 1 to September 1.

*Frequency*: Mostly flying singly and fairly high, but a few closely associated groups, such as 28 on July 15, 55 with many *eresimus* on July 21, and a decided migration of 423 plus on September 1.

*Condition*: Most of the butterflies seemed fresh and new, a few were worn.

*Non-migrant Record*: Mr. Henry Fleming of the Department of Tropical Research staff reports *megalippe* as resident and breeding

[1] Contribution No. 871, Department of Tropical Research, New York Zoological Society.

in the low Valencia plain (circa 450 meters altitude) from Limón to Maracay, and to the north of the pass at sea-level around Ocumare.

*Record*: 1945—July 16 (16 through pass against high wind; 12 low at km. 15). 1946—April 1 (1); May 7 (1 male alighted); September 1 (423 in fairly compact flock through pass). 1948—May 24 (5 seen); June 6 (male taken, 48737), 22 (17 seen twelve feet up), 30 (8 seen); July 5 (6 seen), 6 (15 seen), 8 (3 seen), 9 (10 very high), 10 (6 at pass; 1 taken km. 31), 15 (28 seen), 16 (12 singly), 20 (21 singly), 21 (at least 55 with large numbers of *eresimus;* 2 females taken), 26 (female taken km. 16).

**Danaus eresimus eresimus** (Cramer).

*Field Name*: Southern Queen.

*Species Range*: Central America to South Brazil.

*Subspecies Range*: Venezuela, the Guianas and northern Brazil.

*Field Characters*: Closely resembles *Danaus gilippus berenice,* the queen of the United States. Smaller and darker but occasionally flying with *D. plexippus megalippe.*

*Number*: Total recorded, 5,258. Taken, 16.

*Sex*: Both sexes taken.

*Date*: May 25 (1946); July 21 to 29 (1948).

*Frequency*: Only one was taken in 1946, a season of infrequent observation. In 1948 a sudden heavy migration of at least 5,000 started on July 21. Several hundred passed in early morning, increasing to several thousand from 10 A.M. on. Many seemed tired and rested on foliage and in long grass. During the succeeding eight days less numerous members of this movement were seen and taken.

*Condition*: Although many were weary, no worn specimens were seen.

*Record*: 1946—May 25 (2 taken, 46502), 28 (3 taken). 1948—June 6 (1 taken); July 21 (5,000+ seen; 9 taken), 22 (210 seen), 23 (27 in grass), 26 (1 taken), 29 (4 seen).

### Migration of Lycorinae.

A single member of this second subfamily of the Danaidae used Portachuelo Pass for purposes of north to south migration.

In flight it was indistinguishable from several butterflies of other families, except on days of high winds, when flocks were forced down into the underbrush. The widely radiating scent hairs characterized it in the net or hand, rarely when resting on foliage.

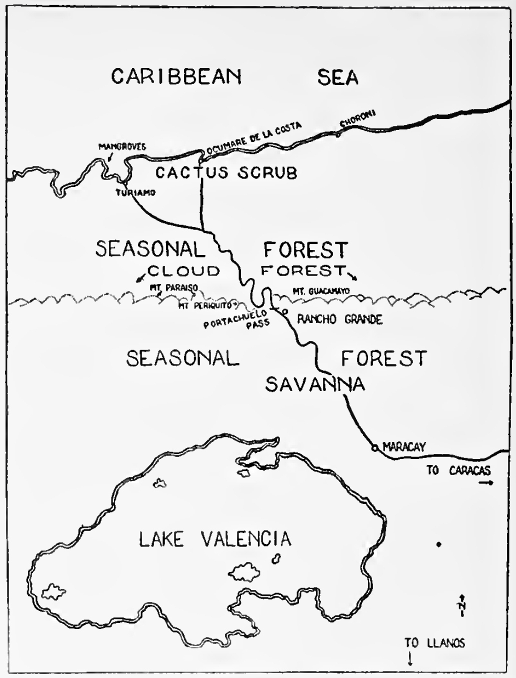
**Lycorea ceres ceres** (Cramer), form **atergatis** Doubleday and Hewitson.

*Field Name*: Tuft-scented Ithomiid-like.

*Species Range*: American neotropics and West Indies.

*Subspecies Range*: Species range, except Cuba and Haiti.

*Field Characters*: Considered the model for a number of mimics. Almost indistinguishable in flight from two ithomiids (*Tithorea harmonia furia* and *Melinaea illis illis*), a heliconid (*Heliconius numata*) and a nymphalid (*Protogonius hippona trinitata*).




TEXT-FIG. 1. Map showing location of Rancho Grande, Portachuelo Pass and surrounding territory.

The swift, bullet-like flight of the latter removes it from too close optical confusion. Once in the hand the almost invariable protrusion of three tufts of black scent hairs identifies *Lycorea.*

*Frequency*: On June 6 a flurry of more than 90 large ithomiid-like butterflies drifted through the Pass, and three taken several minutes apart were all of this species. Four others showed their scent hairs while alighted on melanostomid blossoms, so it seems certain all were of the same species. Nine days later, on June 15, an identical occurrence on a smaller scale took place. A thirty-mile wind blew through the Pass and grounded a host of insects. Among these were 29 Lycoreas. On July 21 a dense flock of at least 32 passed through. Eight other flocks may well have been of this species. Eight were taken singly.

*Number*: Total recorded, 185. Taken, 12.

*Date*: April 30 to July 26.

*Condition*: More than half of those taken or seen showed signs of wear and tear.

*Record*: 1946—May 5 (1 taken at Pass). The following were taken in 1946 at or near kilometer 21: June 11 (female), 23 (female), 25 (male and female), 29 (female), 30 (female). 1948—April 30 (1 taken, 48458), 28 (1), 31 (1); June 6 (3 taken, 90 seen), 15 (2 taken, 27 seen), 26 (2); July 9 (2 taken, 10 seen), 10 (1 taken, 15 seen), 15 (1), 20 (1), 21 (1 taken, 32 in dense flock), 26 (1).

## Migration of Ithomiidae.

Thirty-one species and subspecies of Ithomiidae were recorded as migrants through Portachuelo Pass.

Dr. Wm. T. Forbes lists forty-five ithomiids collected by Dr. P. J. Anduze in "*Del Norte de Venezuela.*" (*Boletin de las Sociedad Venezolana de Ciencias Naturales,* VI, 1949, pp. 308-317). In the relatively minute area represented by the narrow bottle-neck of the Pass we thus took seventy per cent. of the number of ithomiids so far recorded from northern Venezuela.

In a report of the Ithomiinae of Rancho Grande by Dr. Richard M. Fox and Jean W. Fox (*Zoologica,* 32, No. 20, 1947, pp. 173-178) thirty species are listed. Of these all but three have since been recorded by us as migrants, and as these three occur within two or three kilometers of the Pass they should doubtless take their place in the migrant list. I have, however, placed them at the end of the observed migrants. In addition, four species occur as migrants which are not included in the paper by Dr. and Mrs. Fox.

From the point of view of pattern and color the thirty-one species of migrant ithomiids are much more homogeneous than the preceding family of Papilionidae or the succeeding family of Heliconidae. This makes for more difficult, or in a number of cases, impossible distinguishableness in flight.

The species fall into two general types, those typically ithomiine in yellow, black and cinnamon-rufous patterns, and those which have more or less transparent wings, with black or rufous borders. The relative proportion of species is, opaque 14 and transparent 17. This superficial division is strongly reflected and emphasized in habits. The opaque species fly in the open, at lower or higher altitudes, whereas the transparent forms are seldom found away from the shade of the jungle, usually threading their way through dense underbrush. This was especially apparent at the Pass, where a lateral shift of observation of only three or four meters, from open to heavy low growth, would mark the presence or absence of opaque-colored and of transparent patternless species.

The reality of what I have called "typically ithomiine" pattern and coloring is emphasized when we consider such migrants as the danaid *Lycorea ceres ceres,* the nymphalid *Protogonius hippona trinitata,* the heliconid *Heliconius numata numata,* the pierid *Charonias eurytale eurytale* and even the arctiid moth *Pericopis angulosa.* Again and again these unrelated forms completely fooled us in the field, we mistaking one for the other, so remarkably similar are the patterns and colors of these models and mimics.

As to relative comparison of species and individuals, of fifteen species, or about fifty per cent., one to ten individuals were recorded. One hundred to fourteen hundred specimens were observed in only five species, or twenty per cent.

Month after month there was noticed among passing migrants a large number of species comprising very few or solitary individuals. Six examples of this type of occurrence (so characteristic of many tropical organisms) are as follows, each record being made within a period of one to three hours; and all six within forty days' time.

| | | | | |
|---|---|---|---|---|
| June 17, 12 | specimens | of | 10 | species |
| July 8, 12 | " | " | 12 | " |
| July 15, 35 | " | " | 13 | " |
| July 16, 12 | " | " | 10 | " |
| July 21, 50 | " | " | 14 | " |
| July 26, 22 | " | " | 11 | " |

In 1945 and 1946 Mr. Fleming was keenly interested in the composition and habits of dense flocks of ithomiids, in the vicinity of kilometers 20 and 21. The details of this interesting occurrence will soon be published. These flocks of butterflies appear earlier in the year than the first migrants and seem to be resident, but in a number of cases the comparative counts and times of occurrence link them so closely to contemporary passing migrants that I have recognized the apparent identity of origin by inclusion.

### *Eutresis hyperia hyperia* Doubleday and Hewitson.

*Field Name*: Plain Hindwing.

*Species Range*: Central America, Colombia, Peru, Ecuador and Venezuela.

*Subspecies Range*: Venezuela, Colombia and northeast Peru.

*Field Characters*: Large semi-clear forewing, plain, pale brown hindwing. These characters sometimes apparent in flight, easily identified in resting individuals.

*Number*: Total recorded, 70. Taken, 24.

*Sex*: Both sexes taken.

*Date*: From April 24 to September 8.

*Frequency*: Recorded on 16 days, usually singly. The largest number together 28, on September 28.

*Condition*: Mostly fresh-appearing.

*Record*: 1946—April 8 (male, km. 21); July 1 (male, km. 21), 8 (male, km. 21; female, Pass); August 13 (female, km. 21); September 8 (1, 461174; 28 seen driven down to foliage by high wind). 1948—April 24 (1 taken, after being caught and dropped by blue-and-white swallow; 5 at Pass on foliage); May 1 (3), 9 (2); June 6 (5), 18 (1), 19 (1 taken, 3 seen); July 2 (1 seen), 3 (1, km. 27), 4 (1 taken, 481055; 2 seen), 10 (1 taken, 6 seen), 16 (1), 21 (1); August 2 (1).

### *Tithorea harmonia furia* Staud.

*Species Range*: Trinidad, Guianas, Venezuela, Colombia, Ecuador, Bolivia and Amazons.

*Subspecies Range*: Venezuela and Colombia.

*Field Characters*: Large, typical ithomiid pattern, yellow and orange. Indistinguishable on the wing from at least three others.

*Number*: Total recorded, 9. Taken, 4.

*Sex*: Both sexes taken.

*Date*: From May 22 to June 16.

*Frequency*: A rare species. Only 9 recorded in two years.

*Record*: 1946—May 22 (female taken). 1948—May 24 (1 taken); June 15 (1 taken), 16 (1 caught from a group of 6, with one of which it was trying to mate. The group was all worn, alighted close together, so I am considering them of this species).

**Olyris crathis crathis** Doubleday and Hewitson.

*Species Range*: Central America and Venezuela.

*Subspecies Range*: Venezuela.

*Field Characters*: Large, typical ithomiid pattern and color; hindwing plain red-brown with central, oblong, transparent window.

*Record*: Only a single specimen taken.

April 30, 1948. No. 48457. Taken on a sunny day in company of other species of ithomiids.

**Melinaea lilis lilis** (Doubleday and Hewitson).

*Species Range*: Mexico to Colombia, Venezula and Peru.

*Subspecies Range*: Northern Venezuela and Colombia.

*Field Characters*: Large, typical ithomiid pattern and color. Except for larger size (forewing length 43 mm. as compared with 38 mm.), indistinguishable in flight from *Mechanitis doryssus veritabilis*.

*Number*: Total recorded, 55. Taken, 21.

*Sex*: Both sexes taken.

*Date*: April 13 to July 20.

*Frequency*: Seen singly or in twos, except for two groups of 16 and 18. Usually high fliers, so we doubtless missed hundreds.

*Flight*: Usually higher than most ithomiids.

*Condition*: Mostly appeared freshly emerged.

*Record*: 1946—April 13 (female, km. 21); June 10 (female, km. 21); July 3 (female, 46725, km. 21), 8 (2 females, km. 21). 1948—May 13 (1 taken, 48522), 15 (1), 20 (1 taken, 18 seen low and alighted), 23 (2), 26 (3); June 17 (1), 24 (1 taken with pierid and heliconid mimics); July 6 (3 taken, 16 seen close at hand in same group as those captured), 15 (1), 20 (1), 22 (1).

**Xanthocleis aedesia aedesia** (Doubleday and Hewitson).

*Field Name*: Black Hook Ithomiid.

*Species Range*: Central America and northwestern South America.

*Subspecies Range*: Northwestern South America.

*Field Characters*: Large (forewing 38-40 mm.), with large black-bordered pale forewing spots, and black hook projecting downward into mid-hindwing orange. Hook easily identified in flight with naked eye or No. 7 binoculars.

*Number*: Total recorded, 434. Taken, 104.

*Sex*: Both sexes taken.

*Date*: April 8 to August 4.

*Frequency*: Decidedly gregarious, flocks recorded of 15, 19 and 41, up to 135.

*Record*: 1946—April 8 (male, km. 21); May 7 (male, km. 21), 21 (female), 25 (4 taken, 46502), 28 (9 taken); June 23 (3 females, km. 21); July 3 (1), 15 (3 females); August 4 (male, km. 21). 1948—April 30 (4 taken, 48455); May 4 (87 seen A.M., 48 P.M., slow, low flying), 6 (1), 9 (1), 21 (1), 23 (4), 24 (1), 29 (3); June 6 (15 taken), 7 (1), 10 (2 taken, 19 seen), 15 (2), 27 (2), 28 (6 taken, 68 seen); July 5 (1 taken, 12 seen), 6 (3 taken, 32 seen), 8 (1), 9 (41 seen high), 10 (1), 13 (1 taken, 6 seen), 15 (2 taken), 19 (2 mating), 21 (8), 23 (1), 26 (1).

**Mechanitis doryssus veritabilis** Butler.

*Species Range*: Central America and northern South America.

*Subspecies Range*: Venezuela and Trinidad.

*Field Characters*: Typical ithomiid pattern and color. Midway in size of forewing length (38 mm.) between the larger (44 mm.) *Melinaea lilis lilis*, and the smaller (28 mm.) *Hypothyris euclea fenestella*. Otherwise indistinguishable in flight.

*Number*: Total recorded, 133. Taken, 98.

*Sex*: Both sexes taken.

*Date*: April 29 to July 29.

*Frequency*: Mostly singly, otherwise in small groups of 4, 6, 7 and 18.

*Condition*: Very few worn specimens seen.

*Record*: 1946—May 28 (7 taken), 29 (5); June 23 (2 males, km. 21), 29 (male, km. 21), 30 (2 males); July 3 (1 at Pass, 46725; 3 females, km. 21), 7 (female, km. 21), 8 (female), 25 (female). 1948—April 29 (1 taken); May 6 (1, 48497), 8 (3 taken, 3 seen), 15 (1 taken, 4 seen), 23 (4), 24 (7), 26 (16), 31 (5); June 6 (6), 7 (1), 8 (1), 15 (1), 17 (2), 18 (2), 19 (1), 22 (1), 23 (1), 24 (4), 28 (4 taken from swarm of 18); July 3 (1), 4 (3), 5 (1 taken, 6 seen), 8 (1), 9 (1), 10 (1 at Pass, 1 taken, 4 seen, km. 31), 13 (1), 15 (4), 17 (1), 21 (2), 23 (1), 24 (1 at Pass, 1 at km. 15), 26 (2), 29 (1).

**Hyalyris cana cana** (Haensch).

*Field Name*: Black-bordered Clearwing.

*Species Range*: Venezuela and Colombia.

*Subspecies Range*: Eastern Colombia and northern Venezuela.

*Field Characters*: This rare ithomiid is very distinct and easy to distinguish both on the wing and alighted. The wide, white-dotted border surrounding all four wings, enclosing transparent central areas, is unmistakable. Indistinguishable from the congeneric *H. coeno*.

*Number*: Total recorded, 7. Taken, 7.

*Sex*: Both sexes taken.

*Date*: July 14 to 21.

*Frequency*: Very remarkably, in 1948, seven specimens were taken, one a day, July 18 being the only exception to the regular sequence, no insect being captured on this date. They were low-flying, close to the top of the low growth like the other clearwings.

In addition to the 1948 migrants at the Pass, Mr. Fleming took 4 males and a female in the dry season, at kilometer 21. These seemed to be residents, judging by the dates of capture, and were associated with a large swarm of ithomiids of other species. They were taken on February 27 and March 4.

*Record*: 1948—July 14 (1 taken), 15 (1, 481174), 16 (1 taken), 17 (1), 19 (1), 20 (1 taken at ginger blossoms), 21 (1).

**Hypothyris euclea fenestella** (Hewitson).

*Field Name*: Dwarf Typical Ithomiid.

*Species Range*: Central America, Colombia, Venezuela, Ecuador and Peru.

*Subspecies Range*: Venezuela and Trinidad.

*Field Characters*: Typical ithomiid yellow, orange and black. Differs in its small size from other similarly colored species. From the equally numerous and equally sized *Ithomia iphianassa* it differs in lacking the transparent large spots and oblong windows.

*Number*: Total recorded, 488. Taken, 123.

*Sex*: Both sexes taken.

*Date*: April 29 to August 2.

*Frequency*: One of the most abundant species and decidedly gregarious, counts of 54 to 266 being made, and of course many thousands of butterflies missed. On a number of days this was the dominant species.

*Record*: In 1946 Mr. Fleming collected 35 males and 56 females in the vicinity of kilometers 20 and 21. 1948—April 29 (1, 48449); May 21 (2), 23 (1), 25 (14 taken, 54 seen), 26 (2), 29 (1), 31 (1); June 6 (14 taken), 15 (1), 16 (1 taken, 12 seen), 17 (1), 21 (3), 22 (1), 24 (2), 27 (2); July 3 (2), 4 (6 taken, 28 seen), 5 (5 at Pass, 3 taken km. 21), 8 (13 taken, 266 seen), 10 (3 taken, 3 seen), 13 (1 taken, 2 seen), 14 (4), 15 (9), 16 (1), 20 (3), 21 (16), 23 (1), 26 (3), 29 (5); August 2 (2 taken).

**Ithomia agnosia agnosia** Hewitson.

*Species Range*: Venezuela, Colombia and northern Peru.

*Subspecies Range*: Venezuela.

*Field Characters*: This clearwing was quite indistinguishable from seven or eight other species.

*Number*: Total recorded, 23. Taken, 23.

*Sex*: Both sexes taken.

*Date*: April 30 to September 3.

*Frequency*: Solitary flyers and low, just clearing the undergrowth.

*Record*: Only 4 migrants were taken at the Pass in 1948, whereas eighteen were taken at kilometers 20 and 21 in 1946. Dates corresponding as to months, I have included the latter as probable migrants.

1946—April 30 (1); May 15 (1), 24 (1), 26 (1), 28 (1); June 4 (2), 7 (1), 14 (1), 18 (1), 23 (1), 25 (1), 26 (2); July 2 (3), 17 (1); September 3 (1). 1948—May 26 (1); July 6 (1), 26 (2 taken).

**Ithomia iphianassa iphianassa** Doubleday and Hewitson.

*Field Name*: Common Small Ithomiid.

*Species Range*: Venezuela.

*Subspecies Range*: Venezuela.

*Field Characters*: The small size combined with transparent patches and bright colors make this very abundant species easy to identify in flight.

*Number*: Total recorded, 1,403. Taken, 205. Many thousands must have passed unrecorded.

*Sex*: Both sexes taken.

*Date*: April 27 to September 8.

*Frequency*: This species was so abundant that on some days a continuous stream was passing. No condensed flocks but the dominant butterfly on many days. The low counts at the Pass in 1946 due to infrequent observation.

*Flight*: Moderately low and never very rapid.

*Record*: 1946—May 28 (1), 29 (1); July 3 (2), 17 (1); September 7 (4), 8 (3). In addition 109 males and 37 females were taken by Mr. Fleming at kilometer 20 and lower in 1946. 1948—Records are so numerous that I condense as follows: April 8 (1 taken, 8 seen), 28 (7 seen); May (on 17 days, 33 taken, 98 seen); June (on 30 days, 97 taken, 175 seen); July (on 28 days, 75 taken, 925 seen).

**Mileria cymothoë** (Hewitson).

*Field Name*: Small Clearwing.

*Species Range*: Venezuela and Colombia.

*Field Characters*: Small and almost completely transparent, indistinguishable in life from 5 or 6 other species.

*Number*: Total recorded, 12. Taken, 12.

*Sex*: Both sexes taken.

*Date*: May 5 to July 21.

*Record*: 1948—May 5 (1 male), 6 (1 male), 23 (1 male), 26 (5 females), 29 (1 male); June 6 (male), 28 (female); July 21 (female).

**Oleria victorine graziella** (Oberthür).

*Species Range*: Central America, Colombia, Venezuela, Ecuador, Bolivia and upper Amazons.

*Subspecies Range*: Venezuela and Colombia.

*Field Characters*: A small clearwing with strong black borders, indistinguishable in life from six other species.

*Number*: Total recorded, 7. Taken, 7.

*Sex*: Both sexes taken.

*Date*: April 8 to July 10.

*Record*: 1946—April 8 (2), 13 (1), 16 (2); July 10 (1). 1948—May 29 (1).

**Oleria makrena makrena** (Hewitson).

*Species Range*: Colombia, Venezuela and Ecuador.

*Subspecies Range*: Colombia and northern Venezuela.

*Field Characters*: A clearwing with wings tinted with whitish. Only once could I be sure of it before capture; in the sunlight resting on a leaf.

*Number*: Total migrants, 7. Taken, 7.

*Sex*: Both sexes taken.

*Date*: June 6 to July 21.
*Record*: At lower levels in 1946 Mr. Fleming took 51 males and 21 females. These may very likely have been early migrants but we had no definite proof. 1948—June 6 (1), 15 (1), 16 (1); July 5 (1), 6 (2 seen alighted), 8 (1), 21 (1).

**Oleria phemonoë phemonoë** (Doubleday and Hewitson).

*Species Range*: Colombia, Venezuela and Brazil.
*Subspecies Range*: Venezuela.
*Field Characters*: A rare clearwing indistinguishable in life from related species.
*Number*: Total recorded, 11. Taken, 11.
*Sex*: Both sexes taken.
*Date*: May 29 to July 23.
*Record*: 1946—April 8 (2, km. 21); May 29 (2 at Pass); June 20 (female, km. 27); July 5 (male, km. 27), 28 (female, km. 27). 1948—May 27 (1 at Pass); July 8 (1), 23 (2).

**Aeria eurimedia agna** Godman and Salvin.

*Field Name*: Six-lemon-striped Ithomiid.
*Species Range*: Central America, Colombia, Ecuador, Venezuela, Guianas and Amazonia.
*Subspecies Range*: Central America, Colombia, Venezuela and Trinidad.
*Field Characters*: The six elongate lemon spots surrounded by spots make this small species easy to identify even in flight.
*Number*: Total recorded, 56. Taken, 29.
*Sex*: Both sexes taken.
*Date*: April 7 to September 7.
*Record*: 1946—Twenty specimens taken at or near kilometer 20, undoubtedly migrants; dates as follows: April 7, 8, 13, 30, May 28, June 10, 16, 30, July 3, 17, 25, 28, August 13, September 7. 1948—May 25 (2 taken, 16 seen), 26 (1); June 6 (2), 9 (1), 22 (1 taken, 11 seen); July 5 (1), 8 (1).

**Dircenna euchychma** Felder.

*Species Range*: Colombia and Venezuela.
*Field Characters*: A medium sized, translucent, dusky, red-brown species, indistinguishable in life from *Dircenna jemina.*
*Number*: A single specimen, 481392, taken July 26, 1948, migrating through Pass in company with ithomiids of other species.

**Dircenna jemina** (Geyer).

*Species Range*: Venezuela and Colombia.
*Field Characters*: A medium, smoky-brown, translucent species recognizable in life only when it has alighted close by.
*Number*: Total recorded, 52. Taken, 18.
*Sex*: Both sexes taken.
*Date*: March 15 to July 21.
*Frequency*: Taken and seen singly, except on March 15, April 27 and May 13, when 12, 16 and 6 individuals were seen resting close together just beyond reach.
*Record*: 1946—May 3 (1), 13 (1); June 26 (1), 29 (1), 30 (1); 1948—March 15 (1 taken, 12 seen), April 27 (2 taken, 16 seen), 29 (1); May 5 (1), 6 (1), 13 (1 taken, 6 seen); June 17 (1); July 8 (1), 13 (1), 16 (2), 21 (1).

**Ceratinia tutia tutia** (Hewitson).

*Species Range*: Central America, Colombia and Venezuela.
*Subspecies Range*: Venezuela and Colombia.
*Field Characters*: A small, smoky-brown, translucent species not distinguishable from *Hypoleria* and *Godyris.*
*Number*: Total recorded, 237. Taken, 19.
*Sex*: Both sexes taken.
*Date*: May 26 to August 7.
*Frequency*: Seen and taken singly except on August 8, 1946, when a cloud of this species came up to the Pass, after heavy rain, and alighted near by. I took 3 and counted 218.
*Record*: 1946—August 8 (3 taken, 218 seen), 12 (1). (Fourteen males and 2 females taken at kilometer 20 or lower, not counted as migrants). 1948—May 26 (2); June 6 (1), 7 (1), 9 (2), 12 (1), 15 (1), 16 (1), 24 (1), 28 (2); July 8 (1), 13 (1), 21 (2).

**Episcada hymenaea** (Prittwitz).

*Field Name*: Small Brown-veined Clearwing.
*Species Range*: Widely distributed in South America.
*Field Characters*: A very small, brown-veined, patternless clearwing, not distinguishable in life from *Mileria* or *Pteronymia aletta.*
*Number*: Total recorded, 44. Taken, 44.
*Sex*: Both sexes taken.
*Date*: May 21 to July 26.
*Breeding Note*: Female No. 48592, taken May 25, contained many fully formed eggs, with surface sculpture, including vertical grooves and finer markings apparent.
*Record*: 1946—May 28 (1); June 26 (male, km. 20), 29 (2 males, km. 20). 1948—May 21 (3), 23 (3), 24 (3), 25 (10), 26 (7), 29 (3); June 6 (4), 17 (1), 18 (1); July 10 (1), 15 (1), 21 (2), 26 (1).

**Episcada sylpha** Haensch.

*Species Range*: Venezuela.
*Field Characters*: Indistinguishable in life from *Episcada hymenaea,* but very rare.
*Number*: Two specimens only, 1946, June 29, male; and 1948, May 30, male.

**Hypoleria ocalea** (Doubleday and Hewitson).

*Species Range*: Colombia, Venezuela and Trinidad.
*Field Characters*: Small, half smoky, half transparent; not distinguishable in life from other similar species.
*Number*: Total recorded, 4. Taken, 4.
*Date*: May 26.
*Record*: 1948—May 26 (4 taken).

**Pteronymia adina** Hewitson.

*Species Range*: Venezuela.
*Field Characters*: A small clearwing, indistinguishable from others in life.

*Number*: Total recorded, 4. Taken, 4.
*Sexes*: Both sexes taken.
*Date*: May 21 to July 20.
*Record*: (2 males and 11 females taken in March by Mr. Fleming at kilometer 20 and lower. Owing to early date not counted as migrants). 1948—May 21 (1), 25 (1); June 6 (1); July 20 (1).

**Pteronymia aletta** (Hewitson).

*Species Range*: Venezuela.
*Field Characters*: A very small, pale smoky clearwing, hardly to be distinguished in life from several others.
*Number*: Total recorded, 7, Taken, 7.
*Sex*: Both sexes taken.
*Date*: May 24 to July 15.
*Record*: 1946—June 7 (1), 23 (1 taken, km. 20). 1948—May 24 (1), 25 (2), 29 (1); July 15 (1).

**Pteronymia asopo** (C. and R. Felder).

*Species Range*: Northern Colombia and Venezuela.
*Field Characters*: Small clearwing with large white splash. Not identifiable in life.
*Number*: Total recorded, 11. Taken, 11.
*Sex*: Both sexes taken.
*Date*: April 20 to July 17.
*Record*: 1946—April 20 (2 taken); June 29 (2 taken). 1948—June 17 (3 taken), 18 (1), 22 (1), 24 (1); July 10 (1 taken, km. 20).

**Pteronymia beebei** Fox and Fox.

*Species Range*: Northwestern Venezuela.
*Field Characters*: Medium clearwing. Not distinguishable in life from several other species.
*Number*: Total recorded, 14. Taken, 14. (All taken at Pass).
*Sex*: Both sexes taken.
*Date*: May 25 to August 5.
*Record*: 1946—August 5 (1 taken at Pass). Thirty-seven males and 7 females, including type of species, taken by Mr. Fleming at kilometers 18 to 21. 1948—May 25 (1), 26 (3), 29 (1); June 6 (1); July 8 (1), 15 (2), 16 (1), 21 (1), 26 (1); August 2 (1).

**Pteronymia nubivaga** Fox and Fox.

*Species Range*: Northwestern Venezuela.
*Field Characters*: Small clearwing, indistinguishable in life from several other species.
*Number*: Total recorded, 14. Taken, 14.
*Sex*: Males only taken.
*Date*: April 14 to July 8.
*Record*: 1946—April 14 to July 8 (12 males, taken by Mr. Fleming around km. 20). 1948—May 9 (2 taken at Pass).

**Pteronymia veia** (Hewitson).

*Field Name*: Yellow-spotted Clearwing.
*Species Range*: Venezuela.
*Field Characters*: Small clearwing with bright yellow spot.
*Number*: Total recorded, 44. Taken, 44.
*Sex*: Both sexes taken.
*Date*: May 6 to August 2.
*Frequency*: Usually single, but now and then several in association. As with all clearwings they fly low, slowly, just above or more usually threading through underbrush.
*Record*: 1946—May 28 (1 taken at Pass). 41 males and 11 females taken by Mr. Fleming around kilometer 20 and lower, in 1946. Not counted as migrants, in spite of circumstantial evidence. Extreme dates March 8 to July 15. 1948—May 6 (1), 9 (1), 21 (1), 24 (1), 25 (1), 26 (1), 29 (1), 31 (1); June 6 (5), 15 (1), 17 (2), 18 (1), 22 (3), 27 (2); July 5 (1), 7 (1), 8 (2), 13 (1), 14 (1), 20 (1), 21 (3), 23 (1), 26 (3), 28 (1); August 2 (1).

**Godyris kedema kedema** (Hewitson).

*Species Range*: Venezuela and Colombia.
*Subspecies Range*: Venezuela.
*Field Characters*: Medium, pale smoky, half transparent. Often flies so slowly and low that identification is possible.
*Number*: Total recorded, 21. Taken, 21.
*Sex*: Both sexes taken.
*Date*: May 21 to August 2.
*Record*: 1946—June 7 (1 taken at Pass). Seventeen males and 14 females collected by Mr. Fleming at low altitudes to the south of Pass, around kilometer 20, in 1946. Extreme dates were March 13 and August 4. 1948—May 21 (1), 25 (1), 29 (2), 31 (1); June 6 (1), 9 (1), 28 (1); July 13 (1), 15 (5), 17 (1), 21 (2), 26 (3); August 2 (1).

**Pseudocada timna** (Hewitson).

*Species Range*: Colombia and Venezuela.
*Field Characters*: Small clearwing, with much white on forewing. Not distinguishable in life from several others.
*Number*: Total recorded, 7. Taken 7.
*Sex*: Both sexes taken:
*Date*: May 6 to July 15:
*Record*: 1946—None taken at Pass. At kilometer 20, Mr. Fleming collected 16 males and 2 females, the extreme dates being April 8 and July 15. 1948—May 6 (1), 24 (1), 25 (2), 29 (1); June 24 (1); July 15 (1).

**Hymenitis andromica andromica** (Hewitson).

*Species Range*: From Guatemala south through Colombia, Venezuela, Ecuador, Peru and Bolivia.
*Subspecies Range*: Venezuela and Colombia.
*Field Characters*: Medium clearwing with considerable white on forewing. Indistinguishable from others.
*Number*: Total recorded 21. Taken 21.
*Sex*: Both sexes taken:
*Date*: May 24 to August 2.
*Record*: 1946—July 3 (1 taken); August 1 (1 taken at Pass from flock of 19, probably the same species). At kilometer 20 and lower, in 1946, Mr. Fleming collected 66 males and 43 females, doubtless migrants, but not counted as such. 1948—May 24 (2), 25 (4), 29 (1); June 6 (2), 9 (1), 22 (1), 28 (1); July 8 (1), 13 (1), 14 (1), 15 (1), 16 (1), 24 (1), 26 (2); August 2 (1).

**Hymenitis dercetis**
(Doubleday and Hewitson).

*Species Range*: Venezuela and Colombia.
*Field Characters*: Medium clearwing, bright yellow splash. Indistinguishable from several others.
*Number*: Total migrants reported, 31. Taken, 31.
*Sex*: Both sexes taken.
*Date*: April 30 to September 5.
*Record*: 1946—May 28 (1 taken at Pass), September 5 (1 taken). At kilometer 27 and lower, Mr. Fleming collected 72 males and 12 females. 1948—April 30 (1); May 1 (2), 9 (2), 24 (2), 25 (1), 26 (2), 29 (1), 31 (1); June 6 (2), 11 (1), 15 (2), 17 (1), 24 (1), 27 (1), 28 (1); July 3 (1), 10 (1 taken, many probably of this species, seen), 15 (3), 16 (1), 17 (1), 21 (1).

PROBABLE MIGRANTS BUT NOT TAKEN AT PASS.

**Athesis clearista clearista**
(Doubleday and Hewitson).

*Field Name*: Semi-transparent Clearwing.
*Species Range*: Colombia and Venezuela.
*Subspecies Range*: Venezuela.
*Field Characters*: A medium, orange-veined clearwing, very similar to several other species.
*Record*: Two male specimens only taken, and neither actually at the Pass. Two males, 46106, taken February, at Red Bridge, less than one kilometer from the Pass, but in the dry season.

**Hyalyris coeno coeno**
(Doubleday and Hewitson).

*Species Range*: Nicaragua, Colombia, Peru and Venezuela.
*Subspecies Range*: Venezuela.
*Field Characters*: Indistinguishable in life from *Hyalyris cana.*
*Record*: Not taken actually at Pass. In April, 1946, 3 males, 1 female, taken at kilometer 27, north of Pass, feeding on flowers.

**Callithomia agrippina alpho**
(C. and R. Felder).

*Species Range*: Panama, Colombia and Venezuela.
*Subspecies Range*: Eastern Colombia and Venezuela.
*Field Characters*: A smoky clearwing not distinguishable in life from several other species.
*Record*: No specimens taken at Pass and only one near by but lower. A female, at kilometer 21, June 23, 1946.

MIGRATION OF ACRAEIDAE.

The members of this small family seem always to appear at the Pass on days of intensive migration, and in life they are so similar to the smaller ithomiids, as well as to many heliconids, that they were caught and enveloped without special attention. Later, when their true nature was discovered in the laboratory, it was too late to recall flight characters or to be certain of how many others had passed unobserved.

**Actinote anteas** (Doubleday and Hewitson), forms **anteas** (Doubl. and Hew.) and **straminosa** Jordan.

*Field Name*: Striated-hindwing Ithomiid-mimic.
*Species Range*: Guatemala to Colombia, Venezuela, Trinidad and Tobago.
*Field Characters*: Inconspicuous in flight, closely resembling the smaller opaque ithomiids, and even more exactly the heliconid *Heliconius vibilia vialis.*
*Number*: Total recorded, 32. Taken, 32.
*Sex*: Both sexes taken.
*Date*: April 29 to July 26.
*Record*: 1946—July 3 (1 taken). 1948—April 29 (1 taken), 30 (2); May 4 (1), 21 (2, 48546), 23 (3); June 6 (1), 27 (1, 48966); July 3 (1, 481541), 6 (1), 13 (1), 15 (7), 16 (1), 21 (2), 26 (2).

**Actinote hylonome** Doubleday.

*Field Name*: Small White-banded Black.
*Species Range*: Venezuela and Colombia.
*Field Characters*: Small, black, with wide oblique band across each forewing. So resembles other small butterflies and even day-flying moths, that only once were individuals noticed, other than those captured.
*Number*: Total recorded, 20. Taken, 12.
*Date*: April 27 to July 16.
*Record*: 1948—April 27 (2, 48378, 48398; 8 others seen); May 9 (1), 23 (2, 48573), 25 (1), 26 (2); June 6 (1); July 3 (1), 8 (1), 16 (1).

MIGRATION OF HELICONIDAE.

Of all groups of butterflies the heliconids are nearly the most difficult in which to designate typical patterns or colors. In this respect the eighteen species and subspecies of heliconid migrants through Portachuelo Pass seem to have evolved in an effort to resemble species in other groups, to offer themselves as models or mimics, or at least to have developed intensely independent and individual forms.

This, combined with the habit of low flight and slow flapping with much leisurely gliding, makes sight identification in most species a very easy matter.

A key based on pattern and color was of the greatest help in day-by-day recording of numbers, and for what it may be worth to others I reproduce it here. It was of course intended only for my own use with the migrants at Rancho Grande.

**Heliconia** Sight Identification Pattern and Color Key.

Fritillary-like (northern genera; *Agraulis, Argynnis,* etc.)
  Silvery Fritillary—*Agraulis vanillae*
  Dark Silvery Fritillary—*Dione juno*

Large Orange Fritillary—*Dryas iulia*
Dwarf Orange Fritillary—*Heliconius aliphera*
Yellow-banded, Red-hindwing
Solid-red-hindwing—*H. procula*
*H. clysonimus*
Striated-red-hindwing—*H. doris* (form, *transiens*)
Yellow-banded, Blue-hindwing
Large, Blue-hindwing—*H. doris* (form, *doris*)
Small, Blue-hindwing—*H. sara*
Light-striped Black
4-white-striped Black—*H. antiochus antiochus*
4-yellow-striped Black—*H. antiochus aranea*
Zebra-striped Black—*H. charithonius*
Red-banded Black—*H. melpomene*
Acraeid-mimic—*H. vibilia vialis*
Ithomiid-mimic—*H. isabella dynastes*
*H. anderida holcophorus*
*H. anderida semiphorus*
*H. eucoma metalilis*
Green-spotted—*Philaethria dido*

**Agraulis vanillae vanillae** (Linnaeus).

*Field Name*: Southern Fritillary.
*Species Range*: New York to Chile and Argentina.
*Subspecies Range*: Panama, northern South America, Amazonia and Lesser Antilles.
*Field Characters*: The same species as our northern silver spangled fritillary, but several minor characters provide it with a subspecific name, characters impossible to tell on the wing. All specimens taken were characteristic, however. The absence of the dark hue of the underwings easily distinguishes it from *Dione juno*.
*Number*: Total recorded, 188. Taken, 40.
*Sex*: Both sexes taken.
*Date*: May 9 to July 29.
*Frequency*: Usually singly or in twos. On June 22 and 24 great numbers were observed high in air, hundreds of which must have escaped our counts.
*Condition*: A minority only were observed to be torn and faded.
*Record*: 1946—May 28 (1), 25 (1). 1948—May 9 (2 seen), 13 (2), 15 (1 taken, 4 seen), 23 (2); June 6 (13), 17 (2), 22 (many high, 19 counted), 24 (many high, 64 counted); July 2 (2), 5 (1), 6 (11 seen), 8 (2 taken, 17 seen), 10 (1), 13 (1, km. 15), 14 (1), 15 (3), 16 (4), 17 (2, km. 30; 15 seen), 19 (2), 21 (1), 29 (14 seen).

**Dione juno** (Cramer).

*Field Name*: Dark Silvery Fritillary.
*Species Range*: Central America to Brazil.
*Field Characters*: Distinguished from *Dryas iulia* above by broader, darker wings and smaller size, and from *Agraulis vanillae* below by dark setting of silver spangles.
*Number*: Total recorded, 194. Taken, 19.
*Sex*: Both sexes taken.
*Date*: May 25 to September 9.
*Frequency*: Decidedly gregarious, but in moderately sized flocks.
*Condition*: Many worn and tattered specimens, many perfectly fresh.
*Record*: 1946—September 9 (1 taken). 1948—May 25 (1 taken, 8 seen); June 17 (2 taken, 14 seen); July 1 (1 taken, 12 seen), 5 (1 taken, 10 seen), 9 (48 seen high), 10 (1 taken, 19 seen), 11 (2 seen, km. 31), 14 (1 taken, 3 seen), 15 (1, km. 15), 16 (1), 17 (8 seen), 19 (2 taken, 9 seen), 22 (1 taken, km. 35, 28 seen), 29 (21 seen).

**Dryas julia** (Fab.).

*Field Name*: Large Orange Fritillary.
*Species Range*: Trinidad, Guiana and Brazil. Not before recorded from Venezuela.
*Field Characters*: A large, narrow-winged orange fritillary, to be confused only, and that hardly, with the silver-spangled *Dione juno*.
*Number*: Total recorded, 969. Taken, 6.
*Sex*: Both sexes taken.
*Date*: April 15 to September 7.
*Frequency*: On July 18, September 1 and 7, 1946, seven-eighths of all observed specimens of this species passed through the Pass. In the following year only flocks of moderate size were seen.
*Condition*: In many of the flocks the fresh and the worn and faded individuals seemed about equal in number.
*Record*: 1946—May 28 (1); July 18 (450 + seen), September 1 (321 counted), 7 (95 + counted). 1948—April 15 (1), 30 (4 seen); May 4 (3 seen); June 28 (1 taken, 22 seen); July 3 (1 taken, 28 seen), 10 (2 seen, km. 20), 13 (1 taken, km. 15), 17 (3 seen), 21 (4 seen), 24 (2, km. 31), 26 (42 seen), 29 (16 seen).

**Heliconius aliphera aliphera** (Godart).

*Field Name*: Dwarf Orange Fritillary.
*Species Range*: Mexico to Paraguay.
*Subspecies Range*: Colombia and Peru to Trinidad and Paraguay. Not before reported from Venezuela.
*Field Characters*: A diminutive copy of the preceding species, *Dryas julia*.
*Number*: Total recorded, 2,313. Taken, 35.
*Sex*: Both sexes taken.
*Date*: May 28 to September 9.
*Frequency*: As with *Dryas julia*, great numbers were seen in early September, more than half of all observed on September 1, 5 and 7. Hundreds, if not thousands, must have passed unobserved. The majority of this host were faded and torn. Several taken gave out a strong scent of witch hazel, much like that of *Heliconius melpomene*.
*Record*: 1946—May 28 (3 taken); July 3 (1, 46725), 8 (1, 46752), 30 (200 seen); August 12 (411 seen); September 1 (285 in one hour, all worn), 5 (1 taken, 461134; 463 seen, worn), 7 (700 + seen), 9 (1, 461162). 1948—July 14 (1, 481168), 15 (3 taken, 63 seen), 16 (1), 17 (6 seen), 20 (2), 21 (8 taken, 150 + seen), 24 (1 taken, strong witch hazel scent), 26 (1), 31 (1).

**Heliconius procula** (Doubleday and Westwood).

*Field Name*: Red-hindwing Yellow-banded.

*Species Range*: Venezuela and Colombia.

*Field Characters*: With the yellow forewing spots and the solid red hindwing band this species is not distinguishable in flight from *H. clysonimus clysonimus*.

*Number*: Total recorded, 867. Taken, 22.

*Sex*: Both sexes taken.

*Date*: April 29 to September 8.

*Frequency*: A third species in which large numbers appeared in late July and again in early September. At other times they usually were seen singly.

*Condition*: Almost all of those seen were in fresh, unfaded condition.

*Record*: 1946—July 18 (600 + seen), September 8 (3 taken, 461176; 213 seen). 1948—April 29 (1); May 26 (1); June 6 (6); July 6 (1 taken, 6 seen), 7 (1, 481021), 14 (27), 15 (2), 17 (1, km. 30), 18 (1), 27 (2 taken, 26 seen).

**Heliconius vibilia vialis** (Stichel).

*Field Name*: Acraeid Mimic.

*Species Range*: Guatemala to South Brazil and Peru.

*Subspecies Range*: Guatemala to Colombia.

*Field Characters*: Hindwing, black-veined striations on orange; with only forewing double (instead of single) band of yellow spots to distinguish it from acraeian species.

*Number*: Total recorded, 43. Taken, 8.

*Sex*: Both sexes taken.

*Date*: April 29 to September 8.

*Condition*: All specimens fairly fresh.

*Record*: 1946—September 8 (1, 461143a; 13 seen). 1948—April 29 (1, 481442); May 23 (1 taken, 48545; 3 seen), 26 (1), 31 (1); June 28 (1 taken from flock of 10); July 3 (1 taken, 3 seen), 6 (1 taken, 7 seen).

**Heliconius isabella dynastes** Felder.

*Species Range*: Panama to central Brazil and Bolivia.

*Subspecies Range*: Venezuela.

*Field Characters*: So exact a mimic of typical ithomiid pattern that it is indistinguishable in life from several species, especially *Mechanitis doryssus veritabilis*, as well as the heliconid *H. anderida holcophorus*.

*Number*: Total recorded, 7. Taken, 7.

*Date*: June 17 to July 26.

*Condition*: All were in good condition.

*Record*: 1946—July 3 (1, 46725, taken at Pass; 2, 461023, taken at km. 20). 1948—June 17 (1 taken at Pass). July 16 (2 taken), 26 (1 taken).

**Heliconius antiochus antiochus** (Linnaeus), form **alba** Riffarth.

*Field Name*: Four-white-striped Black.

*Species Range*: Colombia to south Brazil and Peru.

*Subspecies Range*: Venezuela to south Brazil and Peru.

*Field Characters*: This black species with its four, forewing, oblique white stripes is unmistakable, except for the rare *aranea* subspecies in which the stripes are yellow.

*Number*: Total recorded, 228. Taken, 39.

*Sex*: Both sexes taken.

*Date*: April 29 to July 27.

*Frequency*: Decidedly gregarious, occasionally singly.

*Condition*: Mostly fresh-appearing.

*Record*: 1946—May 28 (4 taken, 48 seen). 1948—April 29 (1, 48445), 30 (1); May 9 (2 seen), 24 (1, 48583), 28 (1); June 6 (5), 10 (2 taken, 27 seen), 15 (2), 16 (3 taken, 14 seen), 24 (1 taken, 48897; 12 seen), 28 (2 taken, 66 seen); July 5 (3 seen), 9 (3, km. 31), 13 (1 taken, km. 15), 14 (2 taken, 4 seen), 15 (1), 17 (6 seen, km. 30), 19 (2 at Pass, 3 km. 31), 22 (7 seen, km. 35), 23 (pair taken, km. 15), male with strong odor), 27 (1 at Pass, 1 km. 16).

**Heliconius antiochus aranea** (Fab.).

*Field Name*: Four-yellow-striped Black.

*Species Range*: Colombia to south Brazil and Peru.

*Subspecies Range*: Colombia, Venezuela, Ecuador, Guiana and Amazonia.

*Field Characters*: This rare species is not to be distinguished from *H. antiochus antiochus* on the wing.

*Number*: Total recorded, 5. Taken, 2.

*Sex*: Both sexes taken.

*Date*: July 8 to 23.

*Record*: 1948—July 8 (1 taken, 481116), 10 (3 alighted, seen close), 23 (1, 481543).

**Heliconius anderida holcophorus** Staudinger.

*Species Range*: Honduras to Colombia and Venezuela.

*Subspecies Range*: Colombia and Venezuela.

*Field Characters*: A mimic with typical ithomiid pattern and coloring. Indistinguishable from several species, especially close to *Tithorea harmonia furia*.

*Number*: A single specimen, a male, taken, May 21, 1948, at Pass. In somewhat worn condition.

**Heliconius anderida semiphorus** Staudinger.

*Species Range*: Honduras to Colombia and Venezuela.

*Subspecies Range*: Colombia and Venezuela.

*Field Characters*: A large size ithomiid mimic, but with basal half of all four wings rich orange. Indistinguishable in life but closest to *Olyras crathis crathis*.

*Number*: Only a single specimen, a male, taken, July 15, 1948, at Pass.

**Heliconius charithonius** (Linnaeus).

*Field Name*: Zebra-striped Black.

*Species Range*: North Carolina to Brazil and Peru.

*Field Characters*: Unmistakable in its

pattern of yellow and black bands across all four wings.

*Number*: Total recorded, 6. Taken, 3.

*Sex*: Both sexes taken.

*Date*: May 24 to July 21.

*Record*: 1948—May 24 (1, 48584); June 6 (3 seen); July 21 (2).

**Heliconius clysonimus clysonimus** Latr.

*Field Name*: Solid Red-hindwing.

*Species Range*: Costa Rica to Venezuela and Ecuador.

*Subspecies Range*: Venezuela, Colombia and Ecuador.

*Field Characters*: Indistinguishable from *H. procula*, otherwise quite distinct.

*Number*: Total recorded, 90. Taken, 17.

*Sex*: Both sexes taken.

*Date*: May 5 to September 8.

*Frequency*: Usually singly. Only twice seen in any number.

*Record*: 1946—May 5 (1 taken); September 8 (1, 481177; 39 seen); 1948—May 11 (2 seen), 21 (1), 23 (2); June 6 (2 taken, 12 seen), 10 (15 seen), 18 (1 seen); July 2 (1), 3 (4 seen), 13 (1), 15 (1, km. 15), 17 (1), 21 (1), 23 (2 at Pass, 2 on trail), 25 (1).

**Heliconius doris** (Linnaeus), form **transiens** Staudinger.

*Field Name*: Striated-red-hindwing.

*Species Range*: Colombia and Venezuela to Brazil and Bolivia.

*Form Range*: Mexico to Colombia and Venezuela.

*Field Characters*: When flying slowly close at hand or alighted, easy to distinguish from *H. procula* and *H. clysonimus*.

*Number*: Total recorded, 77. Taken, 8.

*Sex*: Both sexes taken.

*Date*: April 29 to September 8.

*Record*: 1946—September 8 (1 taken, 461175; 10 seen). 1948—April 29 (1, 48453); June 22 (6 seen); July 8 (4 taken, 22 seen), 9 (4 seen), 19 (1 taken, 27 seen), 21 (1, 481540).

form **doris** (Linnaeus).

*Field Name*: Large Blue-hindwing.

*Form Range*: Mexico, Colombia and Venezuela to Bolivia and Brazil.

*Field Characters*: Identical with form *transiens* except for color of hindwing. Of this remarkable mutation-like form only three individuals were observed, although it was striking in appearance and easily identified in its slow flight.

*Number*: Total recorded, 3. Taken, 1.

*Date*: July 8 and 10.

*Record*: 1948—July 8 (1 taken, 481116), 10 (2 seen distinctly).

**Heliconius eucoma metalilis** Butler.

*Field Name*: Ithomiid-mimic.

*Species Range*: Panama to Peru and Amazon Valley.

*Subspecics Range*: Colombia, Venezuela and Curaçao.

*Field Characters*: An ithomiid mimic, indistinguishable in flight from several species, as well as from the heliconid *H. antherida holcophorus*.

*Number*: Total recorded, 36. Taken, 29.

*Sex*: Both sexes taken.

*Date*: April 8 to July 26.

*Record*: 1946—April 8 (1); June 10 (1), 16 (1); July 1 (1), 10 (1), 14 (1), 18 (1), 25 (1). 1948—May 2 (1, 481022), 23 (1, 48573), 28 (1); June 27 (1, 48966); July 2 (1, 481021), 3 (2 taken), 6 (1 taken from group of 4, all alighted), 11 (1, 481148, km. 30), 13 (2 taken), 14 (2 taken), 15 (2 taken from flock of 6), 16 (1), 18 (1, 481248), 26 (3 taken).

**Heliconius melpomene** (Linnaeus), form **melpomene** (Linnaeus).

*Field Name*: Red-banded Black Heliconid.

*Species Range*: Northern South America to Peru and central Brazil.

*Field Characters*: A common migrant and resident at Rancho Grande. Slow flyer, usually through underbrush and along trails, easily caught with fingers, always giving out a strong scent of witch hazel. In pattern and color very close to the female pierid *Perente charops meridana*, and to the nymphalid *Adelpha lara lara*. In both cases the wings are broader and the flight nervous and swift in comparison with the heliconid. The three species are sometimes seen associated.

*Number*: Total recorded, 2,566. Taken, 42. Thousands were not counted on days of intensive migration of other species.

*Sex*: Both sexes taken.

*Date*: April 29 to September 7.

*Note*: Never saw them hurrying; often alighting on leaves or blossoms; occasionally courting and mating.

*Record*: 1946—May 22 (1), 28 (2), 29 (1 taken, 6 seen); August 3 (213 flying slowly through Pass); September 7 (6 seen, 461145; first in a month). 1948—April 29 (1); May 23 (1 taken, 30 seen), 25 (1 taken, 8 seen), 26 (1, 6 seen), 31 (1 taken, 27 seen); June 6 (2 taken, 30 seen), 7 (1, 6 seen), 9 (1, 61 seen), 10 (509 counted and many missed; 4 and 5 males hovering over single female. Many alighted on my sleeves), 11 (18 in twenty minutes), 15 (16 seen), 16 (17 seen), 17 (117 seen), 18 (48 singly, 68 in groups), 19 (2 at 8.30 A.M.), 21 (28 seen), 22 (53 seen), 28 (27 seen, one with nymphalid mimic, flying around each other), 29 (33 seen); July 3 (1 taken, 66 seen), 5 (243 singly or not more than 6 together), 6 (2 taken, 64 seen), 8 (1 soaked in rain, 108 seen), 9 (29 at km. 31 headed for Pass), 10 (66 seen), 11 (4 seen, km. 15), 13 (130 seen, 3 at km. 15), 17 (8 feeding on lantana, km. 30), 21 (368 seen), 29 (1 taken, 66 seen).

**Heliconius sara sara** (Fab.).

*Field Name*: Small Blue-hindwing.

*Species Range*: Panama to south Brazil and Bolivia.

*Subspecies Range*: Panama, Colombia and Venezuela.

*Field Characters*: Only to be confused with the very rare *H. doris*, form *doris*, and that hardly, for the latter is a full third larger, although one individual *sara* is unusually large.

*Number*: Total recorded, 3. Taken, 3.

*Date*: April 29 to July 25.

*Record*: 1946—May 29 (1 taken). 1948—April 29 (1, 48445); July 25 (1, 481369).

**Philaetria dido** (Clerck).

*Field Name*: Green-spotted Heliconia.

*Species Range*: Honduras to Peru, Bolivia and southern Brazil.

*Field Characters*: Only to be confused with the nymphalid *Victorina stelenes*, from which it can be distinguished by much narrower, more elongated wings, and by a slow, wavering flight.

*Number*: Total recorded, 625. Taken, 4.

*Sex*: Both sexes taken.

*Date*: March 15 to September 8.

*Frequency*: Decidedly gregarious, five large flocks being recorded.

*Record*: 1946—May 26 (13 passing km. 30), 28 (98 seen), 31 (1 alighted and oriented itself to sun); July 8 (196 seen); September 7 (125 passing slowly but steadily), 8 (250 +, bucking high wind). 1948—March 15 (12 seen); April 15 (16 seen), 29 (1, 48444), 29 (1 taken); June 6 (2 taken); July 15 (1 taken), 21 (1 taken).

# 4.

# Home Life of the Bat Falcon, *Falco albigularis albigularis* Daudin.[1]

William Beebe.

*Director, Department of Tropical Research, New York Zoological Society.*

[This is one of a series of papers resulting from the 45th, 46th and 47th Expeditions of the Department of Tropical Research of the New York Zoological Society, made during 1945, 1946 and 1948, under the direction of Dr. William Beebe, with headquarters at Rancho Grande in the National Park of Aragua, Venezuela. The expeditions were made possible through the generous cooperation of the National Government of Venezuela and of the Creole Petroleum Corporation.

[The characteristics of the research area are in brief as follows: Rancho Grande is located in north-central Venezuela (10° 21′ N. Lat., 67° 41′ W. Long.), 80 kilometers west of Caracas, at an elevation of 1,100 meters in the undisturbed montane rain forest which covers this part of the Caribbean range of the Andes. The migration flyway of Portachuelo Pass, which is also the watershed between the Caribbean and Lake Valencia, is 200 meters from Rancho Grande. Adjacent ecological zones include seasonal forest, savanna, thorn woodland, cactus scrub, the fresh-water lake of Valencia and various marine littoral zones. The Rancho Grande area is generally subtropical, being uniformly cool and damp throughout the year because of the prevalence of the mountain cloud cap. The dry season extends from January into April. The average humidity during the expeditions, including parts of both wet and dry seasons, was 94.4%; the average temperature during the same period was 18° C.; the average annual rainfall over a five-year period was 174 cm. The flora is marked by an abundance of mosses, ferns and epiphytes of many kinds, as well as a few gigantic trees. For further details see Beebe and Crane, *Zoologica*, Vol. 32, No. 5, 1947. Unless otherwise stated the organisms discussed in the present paper were observed in the montane cloud forest zone, within a radius of one kilometer of Rancho Grande.]

## Introduction.

This is a record of observations, during a period of one hundred and sixty-four days, of the lives of a pair of bat falcons, from February 20 to August 1 inclusive, in 1948. Most of the watching was done through open windows from within our laboratory at Rancho Grande, the perches of the parent birds and their nest being in full view, at a distance of about one hundred meters. Methods included the naked eye, a 7 × 30 hand binoculars, and Zeiss giant binoculars of 12, 20 and 40 powers. This last was of course mounted on a tripod, and except when in use elsewhere was constantly in place focussed on the perches or the nest of the falcons, so that instant contact could be made at any desired moment by myself or any member of my staff. With this battery of glasses it was possible to see every detail of color, pattern and plumage of both falcons and their victims, as well as such minutiae as the coiling and uncoiling of the tongue of a still living morpho butterfly held in the hawk's talons.

During two preceding years we had become proficient in sight identification of almost every bird, mammal and insect which entered into the diet of these falcons, and within arm's reach in the laboratory was a collection of skins of the birds themselves, loaned by Dr. William H. Phelps. This collection included all the species of small and medium birds which might possibly occur in the vicinity of Rancho Grande.

*Falco albigularis,* as a species, has an extensive distribution, covering 48 degrees of latitude, from central Mexico, south throughout South America, reaching as far as southern Brazil and northern Argentina at about 27 degrees South Latitude. Two subspecies have been described.

The bat falcon is fairly common throughout much of its range, and is accounted a bird of tropical lowlands, rather than of subtropical elevations. Brief accounts of nests, eggs and food have been published, the latter based chiefly on stomach contents.

The principal contribution of the present account is the data afforded by the opportunity for detailed identification of the diet of this pair of falcons throughout more than five and a half months, and the recording of the rise, development and in some cases decline of various instincts in the young birds.

## Previous Records.

In accord with the reputed limiting of these falcons to areas of low elevation are my notes of their presence at sea-level, at Kartabo, British Guiana. In 1920 I found this species living in dense jungle in pairs, always perched in the tops of the highest trees. The adults were feeding chiefly on honey-creepers, both *Cyanerpes caeruleus caeruleus* and *Chlorophanes spiza spiza.* Three of each of these species were found in an equal number of stomachs. Rufous-throated birds of the year were insect eaters

[1] Contribution No. 872, Department of Tropical Research, New York Zoological Society.

for the most part, large and medium butterflies, giant grasshoppers, together with small flying hemiptera and coleoptera, forming the larger proportion of their diet.

At Rancho Grande I have notes of only two occurrences of these birds, other than the pair under consideration. On July 6, 1945, at nine in the morning, I was seated near the gate of Rancho Grande compound, watching a pair of tanagers in a distant tree, when a sharp *ke-ke-ke-ke* drew my attention, and directed it to a bat falcon in the top of a lofty candelo tree, about one hundred meters away. This was the first record for this locality.

The bird looked straight at me as I shifted the barrels of the big binoculars, then shifted its gaze upward and I followed. High in a air, a flock of what to the naked eye might have been dragonflies, resolved into the entire company of Rancho Grande blue and white swallows, *Pygochelidon cyanoleuca cyanoleuca.* They were completely absorbed in the small hawk, but circling at a safe distance. Occasionally one or two reckless birds would swoop down and rush past in high gear, twittering loudly, but attracting not the slightest attenion.

Every feather on the body of the hawk was frequently raised, shaken and settled, as the bird preened itself. Once a small plume fell out and drifted slowly downward, watched by the owner with complete concentration. Most of the time it stood quietly, the head moving quickly from side to side, bobbing up and down in falcon fashion. During the ensuing hour it called three times, a continued rattling, a shrill, high *ke-ke-ke-ke,* five to twelve times, very fast. Once I heard a variation *whew-ke-ke-ke.* Twenty minutes after first discovery the bird rose, called loudly, circled the tree once and started due north. Every swallow vanished, but in less than a minute the hawk returned to a perch a few feet way and equally high. As it flew over every bird sound ceased in the surrounding jungle. A tree crashed near by and there came a loud hum from a plane over Valencia, but the hawk paid no attention. When a fly alighted near its toes, it was watched closely until it took to flight.

At ten o'clock the hawk left again, this foray, after the conventional wasp-like circle, heading it eastward over the Rancho building. This time it was attended by a streaming comet-tail of worried swallows at judicious distances, all twittering as the hawk flew over their nesting crevices. Again the hawk returned but hardly had it resumed its perch when six more bat falcons circled over, high up, and with loud chittering my bird joined them, fell into their circling pattern, and all disappeared northward, directly through Portachuelo Pass. They were apparently migrants only from lowland to lowland through the flyway.

About a month later, on August 4, a single falcon drifted slowly up Limon valley toward the Pass, but soon disappeared into the thin neblina.

The following is a selection of day by day notes from my journal, excluding all unimportant matter which would gain nothing by repetition, and omitting a number of eventless captures of duplicate species prey.

In the first section, mention of individual prey is by species only, this being in accordance with sight identification. In the final systematic list, the subspecies are added, it being understood that these are based on geographical expectancies.

Chronology.

| | |
|---|---|
| Adult falcons first seen, and mating | February 20 |
| Nest discovered | March 30 |
| Eggs estimated laid | March 1 to 5 |
| Incubation estimated | March 5 to April 5 |
| Hatching estimated | April 5 |
| Week-old chicks first seen | April 11 |
| Last visible down gone | May 5 |
| Young male left nest | May 10 |
| Young female left nest | May 13 |

Bat Falcon Diary.

February 20, 1948: Heard a hawk calling at 7:30 A.M. and later saw a bat falcon with something in its claws alight in candelo tree No. 3. The large glasses showed the prey to be a male eastern swallow-tanager, *Tersina viridis.* The blue plumage filled the air as the hawk plucked out beakfuls of feathers, when suddenly there entered my binocular field a larger bird. With an upward swoop the new arrival snatched the prey, and flew off to the top-most twig of candelo No. 2. She—for that proved ultimately to be her sex—tore away at the swallow-tanager while the male watched, and picked at the shreds left in his claws.

Half an hour later the male flew straight across to the other tree, mated with the female intermittently for fifteen seconds, and then back to his own perch. Both birds left a few minutes before nine.

(Note: Directly south of Rancho Grande laboratory, about one hundred meters distant, were three very tall candelo trees, *Gyranthera caribensis.* No. 1, close to the road, fell in the rainy season of 1947. Of the remaining pair, No. 2 was to become the favorite perch of the female falcon, while No. 3, a few meters to the west, was the male's perch more than thirty meters above the ground, all in full view through the open windows of the laboratory. Both trees were on the northern rim of the steep Limon valley, facing and to the south of Rancho Grande. This valley led downward toward Maracay and Lake Valencia, and in the other direction ended at Portachuelo Pass.)

February 22 and on succeeding four days: Male arrived in early morning and left immediately.

February 27: Both birds on their respective perches at 6 o'clock, the male with a male American redstart, *Setophaga ruticilla,* which he plucked and ate. At 8 the male went to the perch of the female and chittered frequently.

February 29: Birds at 6:30. Later the male brought a female euphonia, either *Tanagra xanthogaster* or *laniirostris*. When plucked and partly devoured it was taken by the female and carried away.

March 1: Both birds at 6:30. Male made two flights far down Limon valley and finally returned with a white-breasted martin, *Progne chalybea*, a bird abundant about Maracay and Turiamo but unkown at Rancho Grande except as a migrant through the pass in late July. The female took the bird at once. Its long wings interfered with her landing and she had to circle and make a second upward swoop to her perch.

March 2 to 13: During our absence the birds were reported almost daily, the male carrying prey, but no definite identifications were made.

March 14: Both birds on their perches at 8:30. They were soaking wet after the night's heavy rain, indicating an exposed sleeping perch. Long and thorough preening, and sun bathing with fluffed-out plumage. The male made a fifteen-minute trip and at 10 o'clock returned with a small bird. As he revolved once or twice on his perch I made out glimpses of the pattern and finally identified a male blackpoll warbler, *Dendroica striata*. The air was filled with feathers as he pulled and tossed them out of his beak. Remiges and rectrices were with difficulty jerked out, but the warbler was completely plucked before the falcon began to feed. From the beginning of the defeathering at 10:05, twenty minutes elapsed before the end of the meal. There remained a head and wingless half-devoured skeleton body with a single leg. He clutched this cadaver in one lowered and extended foot, and at 10:30 yawned widely twice, and shut both eyes for five minutes. At 10:40 he ate some more and dropped what was left of skull and skeleton. I am impressed with his lack of plucking and tearing power compared with that of his larger mate.

He sat quietly until 12:15, made three short flights, capturing a honey-creeper, *Chlorophanes spiza*, and then sat in the heavy rain until his plumage was again soaked. Left at 1 P.M. and the female followed a few minutes later. She had spent the entire morning sitting motionless on her perch.

At 3 o'clock both birds reappeared, the male with a freshly caught female redstart, which the female falcon took from him, plucked and devoured. Even in the midst of violent plucking, both birds, at times, would suddenly stop and watch the path of a slowly falling feather until it was out of sight in the foliage far below.

March 15: Male perched at 6:25 with a male thick-billed euphonia, *Tanagra laniirostris*, in his claws. In ten minutes the bird was cleanly plucked and then eaten. A bit of blood and a feather fastened on the upper curve of the beak and would not be shaken off. Although the stub on which he perched was only about an inch across, and a rather strong wind was blowing, yet the falcon gripped his prey in one foot, lifted the other and slowly and deliberately scratched and cleaned his mandible.

The female made a belated appearance and a futile attempt to snatch the remains of a bird from her mate. She then perched and kept up a violent *ke-ke-ke* at her mate, at the top of her voice, revolving the while and picking at the wooden splinters of her perch. She left soon afterward but returned just in time to snatch a honey-creeper, *Coereba flaveola*, from her mate.

The sunlight was unusually brilliant and through the forty powers lenses the bird might have been perching on my wrist. Partly exposed blood sheaths were distinct and, as I watched, a flat feather-fly slid sideways from beneath the plumage and vanished below the scapulars. When watching the bird uttering its call, I became aware that the first beak and throat effort began definitely before my ear caught the first *ke*, while no visible effort accompanied the final *ke*. I then timed threes *kes* with a stop watch and found their duration summed up as exactly a second. This verified a long forgotten fact that sound travels about three hundred and thirty meters a second. So my estimate of the hundred meters from eye to bird seemed reasonably accurate. When the hawks were very excited or hungry, the acceleration of *ke-ke-kes* put all this estimate of trisyllabic tempo to naught.

March 16: Male around at 6:45 with another male thick-billed euphonia. The female falcon circled for a few minutes, then dived out of sight. After plucking the tanager the male also vanished among the foliage. When one or both birds appear there is a very evident subsidence of sound in the neighborhood and no small birds are visible, but this local alarm soon passes. Birds from blue tanagers up in size, caciques, toucans, parakeets, pay no attention. At 3:30 the male brought a short-tailed swift, *Chaetura brachyura*.

March 21: After our four days of absence I saw the male falcon this morning on his perch at 6:38 with prey. This was plucked beyond specific recognition, except that the short, thick beak and a few green feathers indicated another female euphonia. A high wind, thirty miles per hour through the Pass, made perching on one foot most difficult. As I watched, the bird was blown bodily backward; he swung out over the valley and dived out of sight still carrying the bare carcass.

March 22: Male at 6 A.M. Away until 9:30 when he reappeared with small bird prey but dived into the foliage too swiftly for further identification. On perch ten minutes later, for an hour. He makes a perfect weather vane, and today, with variable winds, faced in turn, north, north by east and east.

March 23: Male at 5:35 A.M. Returned at 6:15 with blue tanager, *Thraupis virens*, thereby betraying the apparent fearlessness

of this species in the hawk's presence. Long periods of watching the horizon and unusual plucking used up an hour in preparation, and it was not until 7:10 that the tanager was denuded of feathers. It was then carried down and away.

Two pairs of blue tanagers have their nests in crevices of Rancho Grande's outer walls, together with the blue and white swallows. This afternoon one tanager was missing from the pair in the eastern wing so I presume it was the victim. This is the first time I have evidence of prey captured in the vicinity of the laboratory. Within a week a new tanager mate joined the single bird.

March 24: Male at 6:05. Two trips without prey. The female came at 7:10, preened for a time and both left, flying northeast over the laboratory. This is the first appearance of the female in a week.

March 25: Male on duty at 6 A.M. Left and returned shortly with a dark bundle of prey which the female took at once. Instead of perching and making a complete meal, she soon dived and swooped up among the mid-foliage of the male's candelo. The big glasses showed her in the dense shade, hopping along a large horizontal branch covered with moss and small orchids, and holding a good-sized brown bat in her beak. The skinny fingers of one wing were moving slightly, and she put her burden down, bit it several times, then wiped her beak. Next she picked it up, carried it a short distance farther along a sloping limb and pushed it down hard, nudging with her beak again and again, between two leaves of a radiating monstera. The rounded head and face and the upright ears of the commonest bat of Rancho Grande were plainly visible, *Lonchoglossa caudifera*, the culvert bat. She flew away, but at 3:10 in the afternoon returned, salvaged her bat, tore at it a few minutes and carried it away.

March 26: The male arrived at 5:30 and at 6:15 returned with a still living male black-headed seedeater, *Sporophila nigricollis*, plucked it, dived and returned with empty talons. Before ten o'clock, in the course of a short flight he caught a female of the same species of seedeater which he ate leisurely. After the meal he faced the sun and I again used the 40-power lenses. I was struck with the separate muscular control of adjacent but pigmentally separated plumage areas. The rufous mid- and lower belly and flanks were often flat and tightly compressed, while the cross-barred breast, upper and lower sides were fluffed out, distinctly raised above the level of the rufous, blowing about in the breeze, wholly unlike the firmly-held rufous.

The male remained on his perch all morning and at 2:05 P.M. turned his back to the sun, spread wings and tail to widest extent, fluffed out his plumage and for fifteen minutes seemed half asleep and making the most of the rare undiluted sunshine. He then preened thoroughly and left.

March 27: Male arrived at 5:30. Quiet until 6:10 when he left his perch and flew around the near side of the candelo; then made three complete circles, gaining height rapidly until he was only a speck, and vanished. In less than three minutes he was back on the perch with a bird. I rushed to the glasses just in time to see the female appear from somewhere, fly swiftly to him, turn on her side, grasp the bird and tear it from his claws while going at full speed. Through the glasses I saw the wings of the prey stretch wide, and put them down as a swift's. I followed her to her own perch. She began tearing the bird to pieces and I soon identified the blue and white as one of our Rancho Grande swallows, *Pygochelidon cyanoleuca*. The feathers began to fly and she ate for some time and then shifted to a perch a few feet higher on the same dead limb. At 6:30 she dropped like a plummet straight down and disappeared in the lower foliage of her mate's gigantic candelo. Search as I might, I could not locate her.

At 7:30 the male returned with an unidentifiable bird, mostly plucked before he brought it to his perch. The female later took it and carried it away. As she passed, a smoky flycatcher which I was watching vanished at full speed into the nearest leaves. The male soon flew southeast toward the first Limon ridge, between Rancho Grande and Lake Valencia. Suddenly it dropped faster than I thought any bird could ever fall.

At 8:05 the female appeared and chittered excitedly.

At 9:00 the male reappeared with what seemed to my eyes a parula warbler. When I checked up on range, I realized that the victim of the hawk was the closely related pitiayumi warbler, *Compsothlypis pitiayumi*. This is the Venezuelan representative of our northern parula, and is an inhabitant of lower, more tropical levels than Rancho Grande. The hawk plucked the small bird and ate bones and all, even swallowing several rectrices. The female watched from her perch a meter above him. After he finished his meal she flew and he took her place. When they are near to one another the difference of nine and twelve inches in size is very evident. Her creamy white collar is paler than his.

At 12:30 the male returned with a dead rufous-winged flycatcher, *Myiozetetes cayennensis*. The female started toward him but he would not relinquish his prey, flew heavily out of sight with it, returning at 3 P.M.

March 28: Male at 6 A.M. At 7 he leapt a foot up and let himself fall straight down. Far down, below the tops of the lesser trees, he passed through a shrieking flock of aratinga parrakeets, then swept up on the opposite side and back to the female's perch. The parrakeets might have been stationary in mid-air as far as speed was concerned. They were too big and too well-armed for even him to tackle. An hour later he appeared with a second rufous-winged flycatcher.

March 29: At 10:05 the male came to his perch and the moment I reached the glasses I saw he had an unusual bird. A white rump

was distinct and I knew it for a swallow, and rough-winged came to mind. Then, little by little, I saw every detail. The falcon plucked slowly and turned the prey all the way around. The tail was emarginate, the rump white, the primaries brownish, and as he began on the secondaries I saw that they and their coverts were edged with white. The head was gone but the body plumage was partly white and partly shining green, unquestionably a white-winged swallow, *Iridoprocne albiventer*. This is a lowland bird, new to Rancho Grande but recorded by Wetmore from El Sombrero. Later in the year we were to see several hundred migrating through the Pass.

The treatment of this prey by the hawk was most interesting and I watched the whole process. For twenty minutes he plucked, in a high wind, working with terrific energy on wing feathers, now and then resting by plucking a few beakfuls of body plumage. The wing got tougher as the larger primaries were reached. The thumb plumes refused to be uprooted as did one or two of the secondaries. The entire wing was torn loose at last and swallowed, remaining feathers and all, with great difficulty. The feathers stuck out of the beak for a time, until by strong effort they went down. The rectrices came out easily, and finally there remained the body, clean and intact. He had nibbled at the top of the breast but practically nothing was eaten but the entire wings. The small legs were torn off and dropped.

At 10:30 the female appeared, circling high up, and chittering. The male watched but did not answer. The prey was held in the left foot which rested on the heel. At 10:34 the female dropped, swerved inward, seized the body and left with a single motion without touching the perch or her mate. She went direct to her perch on the nearer candelo, and with ferocity ate the entire body, bones and all. The intestines came first and then she tore the body structure apart and little by little swallowed it.

After a meal both sexes occasionally indulge in a curious continuation of the feeding motions. They tug at projecting splinters of the stub and even at adjacent leaves. At last the beak is wiped and the bird settles down. Her plumage on this occasion needed much arrangement as if she had been brooding.

There was not the slightest doubt that the male prepared the prey for her. I suspected that he might take it away to the nest, until she appeared and took it. I have often seen him pluck and eat a bird wholly without the nicety and neatness of plucking and leaving the body intact when it seems intended for his mate.

March 30: At 5:45 the male perched with a small tanager, *Chlorospingus ophthalmicus*, swooped down into the foliage of his tree, and at 6:15 returned with the bird plucked and dewinged as before, but the legs intact. He watched and waited for forty-five minutes holding it out in his left foot, with heel on perch. He would gaze down into the tree below him for minutes at a time. At 7 the female came, swooped up, took the bird and ate it. He wiped his beak again and again, and picked each toe clean. The first few times I watched this performance the male appeared reluctant to give up his prey. Now he prepares it and literally holds it out as far as possible from him. It appears as if the instinct of share your catch was incompletely developed at first, but now has achieved a definite routine. Every time the female takes food from her mate she returns to her own perch, calls, and before she begins to tear or feed, she evacuates.

From 8:30 until noon I was at Portachuelo Pass watching a heavy insect migration, and in my absence Jocelyn Crane took over, watching the hawks from the laboratory. She was fortunate enough to discover the nest of the falcons, which for the past month has been in full view from the laboratory windows.

Her notes are as follows;

9:50 A.M. Was photographing the male falcon on his perch with a telephoto lens when he vanished. Five minutes later he returned with a freshly caught bat, looking like the same species which he killed five days ago. He plucked casually at the fur but ate nothing. Saw two flat bat-flies sail away from the fur or wings, both together. At 10 the female zoomed by, making a perfect pickup. She banked back to her tree, to her regular perch while the male disappeared. She ripped off the skin and wings, eating both, one after the other.

At 10:14 she plummeted, then curved over to the trunk of the right candelo, the perching tree of the male. She vanished by the time I had refocussed the giant glasses in the general area, and then I suddenly found her in her nest. She still had the bat and was scuffling around in the shallow, apparently empty hollow, appearing and disappearing, occasionally mumbling the bat. Finally she squatted, both she and the bat sinking almost out of sight.

2:15 P.M. (Beebe takes over). Hawk calling. The head of the female was visible in the nest, no attention being paid to the loud *ke-ke-ke-ke* of her mate. The latter was on his perch with a second bat, decidedly larger and the general orange color made it undoubtedly *Chilonycteris rubiginosa.* He skinned the bat, tore off one wing and swallowed it. Called again and then dived. I followed with the glasses in time to see him reach the nest, swooping up from beneath, and deliver the bat, the female reaching out her beak to take it from him. He perched on the rim for a split second, took off and rested quietly on his perch for an hour.

### The Nest.

Candelo number 3, one hundred meters from our laboratory, was 30 to 35 meters high, and the nest, only now discovered, was about half way up, a large but shallow cavity in the trunk. Many years ago, perhaps in the

course of a great storm, one of the largest branches was wrenched away and fell to earth. This left a gaping wound, which sap and wood set to work to heal. Out-flaring, wavering lips of bark began to curl over the rim, then rot or water or some agent interfered and the still exposed heart wood softened and flaked away. This in no way interfered with continued growth of the enormous bole, but left a semi-hollow, shallow but well cupped, which in the year 1948 was destined to provide a home for our pair of bat falcons.

The setting of the arboreal eyrie was very striking. Three sides of the two-by-one-foot opening were exposed, lichen-covered. Down the fourth side a mass of air-plants cascaded from an enormous burst of foliage, twenty feet above. Within a few feet of the hawks' home were many kinds of lush growths which at the first hint of rains put forth new shoots, leaves and blossoms; orchids flowered, as did bromeliads, jungle arums and tropical mistletoe. Four long, dangling air-roots hung at one side with their beginnings so high up that they pendulumed slowly in the slightest breeze, and when high winds and neblina swirled through the Pass and around the candelos, the vegetable ratlines flapped and thrashed like wrecked rigging.

March 31: At 5:30 the male brought a male black-headed seedeater, and after plucking, gave it to female at nest.

April 1: Male with prey at 10:30. Mr. Fleming reports that this was a large sphinx moth, *Pholus obliquus*. The hawk ate the insect, discarding the wings.

April 2: Male flew with bat to nest without plucking or dewinging it. Later came with a gnatcatcher, *Polioptila plumbea,* which must have come all the way from Maracay.

April 4: Male on perch at 6 with bat. Without dismembering it, he called and the female came and took it to the nest. She fussed about with it for a few minutes, on the rim and inside the nest, then took flight, circled once and alighted on a branch half-way between the nest and the perch of the male. Here she laid it down, shifted it, and finally pushed her way into the leaves of a large bromeliad, and backed out without the bat. Flew back to the nest. This is the second instance of caching unwanted food, bats in both cases.

(Note: from April 5 to 9 no notes were made owing to our absence on a trip to the llanos.)

April 10: Hawk heard at 7 A.M. Fog so dense all day that no trace of candelos, hawks or the nest was visible.

April 11: Hawk on perch at 6:30 with a remarkable yellow grosbeak in his talons. It is *Pheucticus chrysopeplus*, and with its huge beak and heavy body, the streaked back and the white-banded dark wings it gives an appearance of size and weight above that of its captor. I would have given much to see the attack. My only record at Rancho Grande is of a pair feeding in a high tree.

The female hawk was on the nest, squatting low. At 7:15 I heard a chattering and saw the female feeding three young birds. They were good-sized, about a week old and clad in creamy white down. At this distance they had the general appearance and size of recently hatched domestic chicks. They were fed with small bits of meat which the parent tore from the body of the grosbeak. One got less than the others. After five minutes, she stood on the rim chattering, then flew to her perch and evacuated. The babies pushed each other about. One fought to get on top, finally succeeded, turned tail toward the open rim and shot a shower of white lime drops far out, on and over the edge.

The female is now marked by slight lime stains on her longest primaries and outer edges of rectrices, so even aside from her superior size and regular perch she is further distinguishable from her mate.

The deep shade and the distance of the nest from our windows had kept the secret well hidden from us. To the naked eye the nest and the bird on the rim were barely distinguishable when we knew exactly where to look.

April 12: At 10:15 the male bat falcon swung up to his perch in the top of the candelo tree with a swift. Through the 20-power glasses I could see every detail and in every respect of the cephalic pale color it seemed to be the rarest of all Rancho Grande swifts, *Cypseloides cryptus*. There was no trace of the supraloral white spots of *cherriei,* and the area around the base of the beak showed the pale grizzled appearance so apparent in both of the specimens taken in 1946. If the bird had been in my hand I could not have had a better view of every detail. It was slowly and thoroughly plucked and as the female did not appear, the male proceeded to eat the eighth known individual of this swift.

At 12:15 the male was on his perch again and the female was feeding chicks. Subsequent onrush of fog hid everything.

April 13: At 9:50 male arrived with a chestnut and gold tanager, *Tangara arthus*, plucked and dewinged it and called. Female came at once, carried it to her perch, quickly ate head and fore body and carried the rest to the nest. Could see only two young birds. Their eyes seem to have more pigment around them. The parent left after feeding, and yelling at the top of her voice, flew to perch.

April 14: While still dusk, at 5:30 I saw a large swallow-like bird dash past my bedroom window and leaned out in time to see the male falcon swoop back close beneath me and snatch a small bat from the air. The bat seemed to be standing still, so swift was the hawk. The legs went out and the mammal was seized with almost no slowing up in the space of a couple of wing beats. The hawk flapped in a half circle and then effortlessly glided with sheer impetus up to his perch. The fog prevented seeing any details of plucking but something of the kind went on, then the watching female swooped from her

perch, snatched in her turn, and took the prey to her young. A half hour later when I entered the laboratory she was just reaching the nest with a second bat, this one twice as large. She pulled it apart and ate it herself. When finished, she came to the nest rim, and for five minutes never ceased calling. The strong adverse wind kept the sound inaudible until I cupped my hands and concentrated. More angles are now visible on the chicks and the down is less dense. Before leaving she cleaned feet and toes thoroughly, one by one.

April 15: A bat caught early, the female taking it as it was, from the male at 6 o'clock.

At 7:50 male caught a hummingbird. Female snatched it at once, pinched the back of its neck, swung it in her beak for a while, then to nest and fed the chicks. She was through and calling for more all within three minutes. The bird was iridescent purplish-blue on head and breast, green elsewhere, tail bronze and the beak medium long and curved, a male blue-headed hummingbird, *Chrysuronia oenone*.

At 10:05 the male brought a blue-black grassquit, a male, *Volatinia jacarina*. He must have gone far down the Limon valley before finding this lowland species. It was fed to the young. The nestlings now crane their necks up when the parents call.

A second blue-headed hummingbird arrived with the male at 1:05, and this time the female took and ate it all, feathers and bones.

April 16: Male came at 7:10 A.M. and brought a *Tangara arthus* and before he had a chance to pluck, the female had it on a branch above the nest, plucked it and tore off the long primaries with no trouble. She always appears much stronger than the male. She fed it to the young, half plucked. The third, very small, chick only got a bit now and then, and was trampled on again and again by the other two. I thought at first he was a male and the others females, but it is apparent that he is the weakling of the brood.

At 9:30 the male brought another culvert bat, and the female took it straight to the nest, tore it apart and fed fur and all. It was heart-breaking to see how the two stronger stood and pushed and gaped at the expense of the smallest. His beak would come up and as a bit of flesh was offered in the parent's beak the larger ones would snatch it and fairly trample on their weaker brother. He has not lost his egg-tooth, and is hardly half the size of the others. The moment she finishes feeding, she steps on the edge of the nest, calls at the top of her syrinx, cleans her toes and claws and flies to her lofty perch. All small birds in sight leave at headlong speed but soon return. Their fear seems deep-seated but evanescant. Also the male seems hardly ever to hunt within sight of perch or nest.

At 10:30 male caught a red-headed green tanager, *Tangara gyrola*, and it was fed, body feathers and meat, to the young. Her instinct ends with pulling off bits of meat and pushing them into the first available beak. By sheer accident, now and then, when the larger chicks are half choking on a beakful of feathers, the little one gets a piece. At noon another bat appeared, with a repeat performance as of 9:30 this morning. After the rain the rim of the nest is quite free from lime, and the trajectory of the birds is now much higher and stronger, the fine but visible spray of white drops arching high over the nest rim.

At 1:20 another blue-headed hummingbird was caught, and required no dressing or plucking before feeding.

April 17: At 5:20 heard the *ke-ke-ke* and reached the window just in time to see the male dive at a bat close to the laboratory. The bat swung inward with such force that it struck the glass but not enough to stun it. The hawk went on with no stopping or slackening of speed, up to his perch.

At 8:25 he returned with a half-dead giant white-collared swift, *Streptoprocne zonaris*, almost as large as himself. The female took it to her perch, and there furiously plucked wing and tail feathers and about half the plumage. There is no doubt about identification, the long wings, almost as long as the hawk's, the black plumage with the white collar and maximum size of the more common species. The female hawk tore off and ate the wings. This species appeared twice more in the diet of the falcons. In the nest the littlest hawk was not visible.

At 9:50 a partly living white-winged swallow was captured and brought back. The female took it at a higher speed than I have seen before, tearing past, reaching out with all eight claws, and snatching it without effort from the out-stretched foot of the male. Chick number one was still too full of giant swift to open his beak, but number two was ravenous. The female daintily tore off a clean bit of meat, turned her head sideways and pushed it into the open beak. If by chance he got it wedged crosswise she nudged the side of his beak, loosened the bit of food and rammed it down. Finally she ate the remainder, feathers and all, and then hovered the brood. No sign of Dopey. I fear he has succumbed to the cruelty of an unvarying instinct; bringing about the extinction of the unfit.

It is significant the number of migrants the hawk is taking, as if their direct flight southward through the Pass and perhaps the slowing up against the usual updraft of wind gave him an extra shade of opportunity.

At 11:50 male came with bird, female took it, flew to her favorite horizontal, secondary perch above the nest, plucked and ate most of the wings and some bony parts. Then to nest where Number One got four-fifths of the food, only at the end when he was stuffed allowing his larger, Number Two, nest mate to get a small share. No signs of the weakling, Number Three. The prey was a black-faced oriole, *Icterus chrysaetus*, not new to

Rancho Grande, but very common at lower levels.

At 12:40 the male caught a stripe-headed warbler, *Basileuterus tristriatus*. The male plucked and ate wings, and gave it to the female, beak from beak. The two chicks fed greedily although their crops were bulging.

April 18: 11:15. The first prey was caught in dense neblina. The female took it to some hidden perch before we could identify it. No signs of Number Three. The smaller of the remaining two gets the major share. The parent never lets any food stick on the chick's beak, but takes time and care to remove it. When she stands on the rim she systematically cleans her legs and feet, but they still remain blood-stained. The grip which these birds have in their toes when perching is remarkable. Often in a high wind, they will draw up one leg and keep perfect balance and poise, looking around nonchalantly, with only four toes for support.

A dog-faced bat brought at 2:30 and fed to young. Later a blue tanager came close to the nest, climbing up the lianas and searching the tangle of leaves, then coming within two feet of the young hawks, and leaving without haste just before the female arrived. This shows a lack of localization of the source of danger, as the tanager was nesting in a hole of Rancho Grande, a hundred meters away.

April 19: A bat brought at 5:30. An excellent series of views showed it to be the same species as we took in Rancho Grande the night before. It was a white-lined bat, small, with a number of white lines extending over the fur, around the head and down the midback, *Uroderma bilobatum*. We could plainly see the yellowish base of the ear, a character which I had written on the label of the one we took and skinned.

At 2:15 the female was on the nest, facing out, close to the rim with a chick on each side, when a twelve-inch anolis lizard, the green and black banded *Anolis squamulosus*, climbed up the trunk. It made a sudden rush, up and over the rim, and the hawk with a quick movement reached forward and seized it by the head. A single pinch and it was drawn in, torn apart and fed. The chick which got the tail had a difficult time, for that organ had become detached, and began a frantic twisting and turning on its own, wrapping about the face and head of the small falcon. Finally the parent had to help poke and untwist, before it vanished, still wriggling.

April 22: (On our return from Caracas). Female took a culvert bat from her mate at 6:10 and fed it to the young. These have grown appreciatively. Although still entirely covered with grayish-white down, the wing feathers project about an inch. The size difference is pronounced, probably sexual, the smaller seeming stronger or more active than the other. The faces are light leaden blue. They are alert, watching every bird or other creature which comes within view, now and then lifting flabby, heavy wings and flapping them as much as possible in the confines of the nest. They have, from the first, showed the vertical head bobbing of the species, as they change the direction of concentration. The whole morning was solid fog, and both adult birds sat close together on the female's tree. Later a pair of blue tanagers perched and searched for insects almost at the entrance of the nest, with both chicks looking at them. A hawk in flight would send these tanagers tearing for cover; a perching one would hold their attention and suspicion, but they seem to see nothing wrong about chicks and nest. The young now call like the parents but weaker, and have lost their baby cheeping.

3:12 P.M. Male caught a blue and white swallow, dewinged and beheaded it, eating these parts, and called intermittently for ten minutes. At 3:30 the female, who had been on a perch below him, taking no notice, finally came ambling on foot along the branch separating them and took the prey from his beak with hers. Flew off, circled and returned to her regular perch. For ten minutes she kept her foot on it, yelling now and then. At last she cached it in a bromeliad above the nest and returned to her perch.

Throughout this time the young were gorged, sunk far down in the nest, their nictitating membranes pulled far over.

April 23: At 5:45 the male was on the female's perch with a small bat which she soon took and fed. At 6:30 he had a female seedeater. At 7:30 the male brought and female took a golden siskin, *Sicalis flaveola*. In the skinning process all the loveliness of the greenish-yellow, orange and bright clear yellow came into view. This is a lowland bird. She fed it after removing only the large wing and tail feathers. A *Tanagra musica*, a black-throated euphonia, followed within a half hour. I was uncertain about the black throat and wished I could see it, whereupon the hawk held the entire bird up in her raised foot, and, with me, gazed steadily at the throat and lower parts! Again and again we should never have been quite sure of species or sex were it not for the deliberateness of the preliminary examination, and the fact that the wing feathers were the first to be removed, leaving in full view all the other portions of the plumage. At 8:55 a turkey vulture swooped low over the road and nest and the female flapped high, dived full speed and struck with talons, spang on the great bird's back. The vulture left hurriedly. At 2:15 a bat was brought and fed, and soon afterwards a black-headed seedeater was caught. These birds are lowland species but are fairly common on upland intrusions, living and nesting in the small patches of grassy open clearing along the winding road.

April 24: Several series of outcries proved false alarms, male and female sitting quietly, while yelling with all their might. We missed the early feeding. Mr. Fleming was walking along the road several kilometers down hill when a head-and-wingless swift fell at his feet, the hawk passing on out of sight. This

circumstantial evidence makes it possible to add another species to the list of prey, a chestnut-collared swift, *Chaetura rutila.* Two more individuals were later included in the diet.

April 25: Bat brought at 6:30. At 7:10 the male came yelling with prey. Female dived, swooped in a large circle and took the bird. Sat quietly, now and then holding up the bird and looking at it. All this fuss concerned only a small, female, curved-bill green hummingbird, *Chalybura buffonii.* The length and curve of the beak, the general size, the light gray under parts, were as distinct as if in the hand instead of one hundred meters away. The female plucked head and wings and then took the trouble to swoop to the nest and offer a chick the half beakful which remained.

Both parents perched for some time. Then the male aroused and went through his regular routine. He shook his head, did a single circle pattering dance on his stub, and concentrated. He bobbed in all directions but chiefly in the direction of the valley to the south. Three times he bobbed, each time four or five ducks of the whole head. He then shot off, flapped rapidly, evidently lost sight of what had attracted his attention, and returned. When he returned empty-taloned he never called. At 8:10 both birds left in a hurry and overtook a big black eagle, *Urubitinga urubitinga,* both in turn striking it feet first. The great black bird ducked and dodged, but three times the falcons rose and fell upon it, until it dived for the shelter of the trees in the valley jungle. Later, the male caught a magnificent black, gold and turquoise mountain tanager, *Compsocoma flavinucha,* and ate it himself.

April 26: A bat and a black-spotted green tanager, *Tangara chrysophrys,* comprised the morning's larder. Both birds left at 11:15.

April 27: At 5:45 the female had a large frog in her claws which the male had just brought. Glimpses made it certain that it was a zipper-backed frog, *Gastrotheca ovifera.* She carried it to the nest but the chicks did not feed while I was watching. I was sorry for this lack of verification of whether this amphibian was edible or not. An hour later she brought a plucked and evidently stiff corpse of a small bird. It had no appearance of recent killing and I can only surmise that it was a cached prey which she had hidden some time before, if not the afternoon of the preceding day.

April 28: At 6:15 the male brought a chestnut-collared swift which the female took, plucked, ate most of the head and then fed to the nestlings. At 7:15 the male returned and the female met him, calling loudly, and took a hummingbird, *Phaethornis augusti.* Plucked carefully it made only about two bites, one for each chick. After she has plucked a bird, large or small, the female may swoop down to the nest at once, or sit for many minutes, waiting until immediately after an evacuation.

The young have grown rapidly and become dull grayish-white, owing to the growing feathers. They continually preen all over, and even one another. Each has a dark cap on the center of the crown, and the legs and feet are strong and bright yellow. All of the major pterylae are now distinctly visible through the ragged down.

The bobbing, almost from the first week, is continuous. The head is turned, the glance fixed in a certain, definite direction and instantly there is a vertical bob or two of the whole head. Then the head is turned quickly toward one or the other side, and another series of jerks takes place. It is as difficult to account for as the foreleg patting or paddling of the lizard *Cnemidophorus,* or the slight withdrawing of the head and refixing of concentration on the same object as is customary in owls. All shifts of vision in the falcons take place in quick sideway turns.

April 29: A bat was brought at 6:15. Another sortie resulted in a male *Tanagra xanthogaster.* At 9:15 the female had vanished, the chicks were fast asleep, and the male was on his high perch. Eight short-tailed swifts rushed past, close to him, but neither species paid the slightest attention. A perching hawk and the same bird high in air above are two very different factors in safety or danger, in relation to possible prey.

At 11:15 the male brought a white-breasted martin, *Progne chalybea.* This is only a casual migrant, so the hawk must have brought this exceedingly heavy bird from far down the valley toward Maracay.

2:45. Note by Miss Crane: The hawk brought two hummingbirds of the same species within twenty minutes, the female taking both. They were both male racket-tails, *Ochreatus underwoodii,* breeding along the ridge at Portachuelo Pass. All four rackets were uninjured when they were brought, before plucking.

April 30: The male came at 7 and the female left. For ten minutes he continued his dance. He half raised his wings, then whittled his beak; turned a little and repeated. This continued until he had made two complete circles, sharpening and scraping on first one, then the other side of the perfectly clean mandibles, eyes closed, and rubbing with all his might. It seems to be some strange nervous preceding of hunting.

At 7:45 he left and in a short time returned with a rough-winged swallow, *Stelgidopteryx ruficollis.* It seemed a bad day for this species for a few minutes after ten he caught another.

May 1: The down on the chicks is now reduced to narrow lines of pale gray, the rufous collar and breast are distinct. First one, then the other waves the wings frantically, each in turn squatting out of reach of the other's waving pinions. There is no doubht about the pair being brother and sister, judging from relative size. At 8:30 another white-breasted martin was provided. Again and again I watch the male set a straight course down Limon valley and keep on until quite out of

sight. This must bring it into the lowland, tropical, martin territory. A bat was brought back at 10.30. The two most common species of bats which have formed a considerable portion of the food are both culvert bats, by which I mean that they roost during the day by preference singly or in clusters under the numerous culverts which guide various streams and brooks across the road. Twice I have seen the male falcon dive at these places, once passing through. At neither time did he pick a bat off the walls, but this circumstantial evidence plus the late hours in the day when bats are captured indicate that this source of manna is frequently used. In early morning I have already told of seeing the hawk take bats from mid-air in front of the laboratory. In this case the bats were snatching moths from the window glass.

May 2: Saw one of the chicks tearing up a good-sized, almost unplucked prey in the nest. There is less and less of careful preparation of the food on the part of the parents, the change nicely geared to the increasing ability of the young hawks to pluck and tear for themselves. The male clings more and more to the lateral sloping rim at one side and above the floor.

May 3: Female arrived at 5:45, called and did her food dance, revolving twice on her perch. She looked for the male, the only time she fails to bob, and he soon arrived with a vireo, *Vireo olivaceus*. At 6:28, with the female sitting quietly and the chicks with full crops, he appeared and called, this time with a male violet and yellow siskin, *Spinus psaltria*. The male ate most of it. At 10:15 she fed one chick with a racket-tailed hummingbird, a male. She left; both chicks edged toward the rim, yawned in concert and went to sleep.

May 4: At 5:45 the female arrived and went through a frantic hunger dance, revolving and tearing at the branch stub beneath her feet. Male brought a culvert bat which was fed almost without plucking. Twenty minutes later a hummingbird was brought, and the female took it and held it in her beak for five minutes. It was then shifted to the left foot. She evacuated, gazed at her prey, and with almost a single motion swallowed it whole. It was one of the smallest of Rancho Grande hummingbirds, a female short-beaked *Chaetocercus jourdanii*. A skin on my laboratory table measures only 69 millimeters.

The young now exercise regularly and alternately, one climbing up the left side, giving room for wing exercise of the other. Five minutes later they will usually have changed places. They seem to find titbits on the nest floor or at least do a lot of searching. The prey is torn or plucked less and less each day. When the parent does tear the prey apart, the separated piece is snatched from her beak at once. Late in the morning the male brought a male racket-tailed hummingbird.

May 5: There is little to choose in size between each parent sex and the corresponding nestling. The throat and three-fourths collar are rich rufous, justifying the old synonym *rufigularis*. The corresponding parts of the adults are creamy white. When the young wings are spread, the blood sheaths are plainly visible, but the tail seems almost full grown. Saw the smaller, the male, tentatively put his foot on the rim, lean forward and look down, then hastily draw back and scuttle behind his sister. A dog-faced bat and a blue-and-white swallow were early morning food. Again and again I notice that when the female is watching for the return of her mate, she never bobs, only turns her head sideways and up and down, scanning every bit of sky. But when looking for prey or danger or down at the nest both she and the male bob continuously, and the chicks never stop.

At 11:14 the male brought a bird, tore off the head and one leg and devoured them and the female then carried it to the nest. The bird was a female American redstart. She hesitated a moment and then left the rim of the nest, carrying the prey. At 1 P.M. she returned with the same beheaded redstart, dropped it in the nest and watched the chick on the floor and the female clinging to the side. When one of them began to tear at the bird she left.

May 6: Hummer caught at 10. Female pulled out a few feathers and left it at nest. It was a male *Anthracothorax nigricollis*. Both young birds now come occasionally to the rim and look down for a long time, then hustle back. The male flopped from his eighteen-inch upper lateral perch down to the floor, knocking over his sister in the process. Within a half hour's time the male brought a white-lined bat and a ***Tanagra laniirostris***. The latter he ate himself.

May 8: Bat taken from male at 5:25 and fed. At 7:40 he brought a diminutive hummingbird, *Chlorostilbon aliciae*, tore off head and ate it, removed a few wing feathers and swallowed all the rest. The young take turns now sitting on the rim and flapping.

At 10:15 the young male was tearing at something in the nest, and lifted it. It was a male black-headed seedeater, *Sporophila nigricollis*. None of the wing feathers or rectrices had been removed.

At 4:20 Miss Crane called out that the male had prey. I reached the glasses in time to see a large, flat wing twist and fall, giving a brilliant blue heliographic flash in the sunlight. It was a fore wing of the only Rancho Grande morpho butterfly, *Morpho peleides corydon*. As I watched, the second forewing fell, and then the two hindwings dropped into the leaves of an airplant below. The male watched them spiral down, and then ate the body of the insect. This was unexpected, and another proof of the swiftness and accuracy of the hunting power of this falcon.

May 9: An almost untouched blue-and-white swallow was brought to the nest at 8:20 and the nestlings tore it apart by themselves and devoured it. At 8:30 the female called from her perch and took another bird

from her mate and ate it all. It was a female bronze-tailed hummingbird, *Aglaiocercus kingi.*

The sun was out strongly and with the 40-powers I examined the colors. There is not the least hint of white in the collars of the young falcons; the belly and flanks are cinnamon-rufous, and the breast collar is apricot buff. This color extends almost around the neck, a half inch at the nape representing the break in what would otherwise be a complete ring.

At 8:43 the female brought a mouse, probably the common jungle mouse, *Heteromys anomalus.* This she tore apart and fed with as much care as she showed in the first week of their lives. This time the young male got the first five pieces, then retired with bulging crop, and his sister filled up. The head was torn off and swallowed by the parent, whereupon she left. She simply leans forward over the rim, drops with closed wings, and in about three of her lengths the wings open and she is in the full impetus of flight. It looks so easy to me, and perhaps to the youngsters, who follow to the rim, flap, look, bob and turn back. At 2 P.M. she brought a gray-breasted swift, *Chaetura cinereiventris,* after plucking, and the nestlings did their own tearing apart. As I watched, I distinctly saw the mass of small ants when the crop and stomach were torn apart, and even several large marble-like abdomens of *Atta* queens, which were eaten by the small hawks.

May 10: This proved to be the fateful day, marking the break-up of the nesting of the bat falcons. At dawn I came down to the laboratory and started watch. At 5:30 the female came to her perch, and the male brought a short-tailed swift. It was carried to the nest and both birds fed on it.

At 6 the male caught another swift which was taken to the nest where the female picked it almost clean. Had continued perfect views of it; a white-spotted swift, *Cypseloides cherriei.* This was one of the nine birds recorded at Rancho Grande, making in all twelve known of the entire species. On his arrival the male falcon held the bird in his talons for several minutes, with the dangling head in full view. There was hardly any chin white, but very large and fluffed-out eye spots.

As happens sometimes in over-anticipated crises, the actual event came and passed almost unnoticed. I left the glasses a few moments and when I returned I saw, without emotion, the female leave the nest. When too late, I realized that it was the rufous-collared male nestling who had dropped from the rim, the remaining bird being the conservative sister. I swiveled up to the candelo perches in time to see the youngster make a crash landing—a messy five-point landing with outspread wings, tail and legs—in a clump of airplants. Slowly collecting his limbs and their feathers, he took off again, fluttered waveringly to his mother, upset her, and clung with agonizing flapping to her perch, and finally made it. He now did three things—looked at distant Lake Valencia on the horizon, chittered *ke-ke-ke-ke,* and bobbed. Life had really begun.

> [NOTE: In order to effect ease of recognition and clarity of distinction, which are the principal objects of nomenclature, from now on I shall use the following terms: adult male falcon—Male; adult female falcon—Female; young male falcon —Bob; young female falcon—Nod. Q. E. D.]

At 6:30 the female swooped back and forth around the perch to which Bob was still glued. She then dived with great speed beyond her candelo down the valley and a few seconds later came fluttering up with a bird, the first we had ever seen her catch since the beginning of the nesting. She held it for a time, then half plucked it, ate the head and went to her favorite branch, pushed it down among bromeliad leaves and returned to her perch. The bird was the warbler, *Basileuterus culicivorus.* Both adults now made swooping circles around the candelos. At 6:40 she returned to her prey, retrieved it and carried it to the nest where Nod disposed of it.

From 7:03 we watched the remaining nestling. It was a period of great emotion, the strain of the pull out into the great world, versus the safety of the nest. The bird would balance on the outer rim, with wings half raised, teetering forward on her toes, almost go, then turn back. Then would ensue a period of violent flapping, in as wide an arc as the confines of the nest permitted.

She would climb to the top of the side wall and pretend to swoop on some prey, a bit of left-over food on the floor, and finally while the fine frenzy lasted, again step to the nest edge, duck and bob, and gradually subside into a yelling mound, crouched on the bottom. The trigger was not quite set. Meanwhile both parents and brother were out of sight high overhead, with no encouraging calls or even casual visit, or any show-hows.

At 7:40 the male swooped southeast toward Guamitis and returned in three minutes with a hummer, *Chlorostilbon aliciae,* which he ate complete, head, bill, all. Off he went and at 7:46 brought another hummer which the female took. This was *Chalybura buffonii.* At this moment the young bird, Bob, flew across the gulf to near the top of his nesting tree, not far below where the male was perched on his favorite topmost stub. The female brought the remains of the hummer to him. He had landed in a mess of smallish dead twigs and slipped and slid, trying to change the bird from beak to claws. But it was too much and the prey slipped and fell far down through the leaves, probably to the ground. He then found a small smooth area, surrounded by small bromeliads and some tiny-flowered orchids. He had a grand time climbing up and down, into the bromeliads, pecking at

lichens. A circling fly occupied all his attention and he almost twisted his head off trying to follow it. Then he preened.

Meantime the male left twice, flying far out over Limón Valley, and dropping like lightning to the tree-tops, but returned without prey. This was at 8:30, and again he went and failed to kill. At 8:55 a red-headed green tanager, *Tangara gyrola*, hopped about just behind the young hawk, arousing not much more interest than had the fly. But when the male returned, the tanager fled with every bit of wing power. The young bird now discovered a distant turkey vulture, and squatted and bobbed as if he was about to take to wing and attack the strange creature. At 9:12 the vulture approached and the female drove it headlong away.

At 10:55 the male came with a blue-and-white swallow and the female took it to Bob, on his broad, horizontal branch. He ate about half and accidentally dropped the rest. When the female came near to watch the eating, Bob turned his back and chittered. Then she went to a slightly higher branch and Bob followed, foot over foot, parrotlike. He came very close and yelled for more food. Twice she moved and he followed.

At 11:10 she swooped down, took a quick look at the nest and Nod and left, leaving a furor of flapping and pseudo-preparation for flight, with no result. Nod seems afflicted with incurable hypsophobia. Noon, no change; everybody preening.

At 12:10 Bob got up to the top perch of the male, and took up his stand no more than an inch or two away. There he remained, staring at his parent and yelling unceasingly. Parent, from my human view point, looked embarrassed and nonplussed, and gazed everywhere but at his offspring. It was amusing and at the same time very interesting that Bob, who had never seen or been fed by his father, should choose to go not to the more accessible female's perch, but laboriously clamber up to the male.

At 12:30, practically pushed off his perch, father fled, followed awkwardly but persistently by Bob, the latter circling twice with his father in mid-air and then collapsing in his mother's tree. Again Bob tried to approach his male parent, but father was fed up and refused to budge or pay attention to his clamoring issue. Bob at last flopped to his more horizontal, comfortable branch where he had eaten his first meal. At 1:50 Bob flew to his mother, knocked her off and alighted. From now on neblina prevented all observation. Late in the day I saw Bob fly into the heart of his mother's tree.

May 11: 5:15 Bob yelling like mad.

5:30 male brought bird, female plucked it thoroughly and fed to Bob who was still in the heart of the tree. The prey was a *Coereba flaveola*. Bob later flew out to a branch between those of his parents.

At 6:15 the female flew to nest, went in and looked at Nod, stayed a moment and left. Five minutes later returned with partly plucked calliste, the black-spotted *Tangara chrysophrys*, and Nod fed on it.

At 6:30 Bob flew down near nest, then into it. He took the remains of the calliste from Nod, and cowered over it in a corner, tore it apart and devoured what was left. Then he climbed up the slanting side of the nest, and before he flew, soiled Nod's plumage with a shower of lime. He had experienced only twenty-four hours of freedom, yet in this short time he had lost the mutual, or at least not unfriendly sharing of food, as well as all directive instincts of nest sanitation.

7:15 male brought hummingbird, female took it and ate it all, a small *Chlorostilbon canivetii*. The color characters showed distinctly. At 7:25 the female herself caught a Rancho Grande blue-and-white swallow, brought it to nest and both birds fed. At 7:35 male caught a *Chalybura buffonii*, took it to his perch and ate it all. It came from near a flowering tree, some distance down the road, greatly haunted by birds of this family. It may be that the abundant supply of hummers was taken as they fed from jungle trees. 7:40 both young in nest preening. Adults circled trees several times, calling loudly. At 8:05 Bob out into the thin air and alighted near the male.

8:20. Male left and flew out over Limon Valley with his swift-beating flight, a very rapid beating of wings, followed by a space of slower beats, then repeated. I followed him with No. 7's. Before long I saw him waver and dodge; then four birds of his own size swooped at him, two or three times. Once he turned sideways and I could see his out-stretched claws. He seemed to turn back and I lost him, but the four birds flew toward me and passed north directly over Rancho Grande, a quartet of white-collared giant swifts. Not very long ago he had brought one of these birds to the female. Apparently they are not afraid of him when on a level; they can probably outfly and out dodge horizontally, but when he has elevation, with the lightning-like speed of his plunge, it would seem that no flying creature can escape. He was back on his perch within the minute.

8:45. Bob returned to nest and ten minutes later left again. He returned twice more to the nest. Actions of all obscured by neblina.

4:00 P.M. Male caught, female plucked and fed a *Tangara arthus*. Both young in nest. Bob seized it and hovered over it in a corner, and after the female left, every bit that Nod got was only after a struggle and a severe tussle. All tolerance and friendly sharing were gone after a few hours of the wide world. His whole psychology was changed. Yet sufficient independence had not been acquired to prevent a return to the nest.

For an hour or two in the afternoon Bob perched on the topmost stub usually occupied by the female.

May 12: 5:15. In the dusk Bob called loudly.

5:25. In dim light, male brought a culvert bat, female ate some, then carried it down to the nest to Nod.

6:00. Bob now appeared, damp and dishevelled, having apparently spent the night in the open. He flew to the long oblique bough in female tree, and ascended it by fits and starts, half like a woodpecker, half like parrot, then flew, pushed off the female and on to the highest stub of the tree.

Male made several forays. When he returned empty-clawed he did his frantic dance of sharpening his beak, revolving several times on top of his narrow perch. Then he brought a short-tailed swift, ate half and the female took it and ate the remaining half. Bob yelled continuously. He can fly well in wide circles but makes terrible landings, especially crashing in thick foliage. He soon stopped calling, so must have had a meal while I was away from the glasses.

8:50. Second bat brought, male to female to Nod in nest.

9:02. Female caught big cicada and ate it. I had heard the loud zzzzz of a "six o'clock bee" stop suddenly in mid-roar, and it may have been this individual. Wings not eaten.

9:40. Very small hummer with a short, almost straight beak; another *Chlorostilbon canivetii*. Male to female. She plucked all long feathers, flew to Bob ten feet away and thrust it at him. He spent much time yelling and looking in all directions before he ate it.

11:06. Male caught hummingbird, gave to female who plucked it and carried it to Nod in nest. Male *Chrysuronia oenone*.

4:30 P.M. In gaps of swirling neblina saw both young in nest.

May 13: Early this morning we heard an uproar of chittering and at 6:00 through the glasses we saw the nest was empty. Nod had flown at last. Later we saw her high up near the female's regular perch. 10:05. Male brought a mockingbird, *Mimus gilvus*, to his perch, plucked off a few tail feathers and the female took it and vanished in the heart of a mass of airplants in her tree. The hunter must have gone beyond the limits of the National Park, even to Limon, to get this lowland species. Neblina shut down on further observations.

May 14: No chance of naming birds brought to youngsters. Rain and neblina opaque. At 6:10 this evening, when sky cleared for a time, saw Nod back in nest.

May 15: Took glasses to bedroom, and in morning saw female come to her perch exactly at 5:30 A.M. Nod left the nest and alighted below female five minutes later. Then the old and young males arrived. The parent made six dives in the thin neblina before he caught a *Chlorospingus ophthalmicus*. Gave it to female who gave it to Nod, who ate for a short time, then Bob took it and finished it.

The difference between the ages are the pale throat and collar of the adults and the yellow of the old ones instead of bluish cere. Twice the young flew against the old birds and dislodged them, yelling for food. Once the young followed the old male in flight, but when the parent wished to lose the youngster, he side-slipped and turned like a streak, leaving his offspring floundering in mid-air.

On the other hand, the most interesting thing of this morning was the occasional brushing off of their perch of the young birds by the parents, a very evident intention to get them on the wing, again and again.

At 7:30 the male caught a female *Anthracothorax nigricollis*, followed by the regular routine of female plucking, eating head and giving the rest to Nod. As she was eating it I saw two birds shoot past at great speed, and the next glimpse showed the male falcon in pursuit of giant swifts. A moment later the falcon returned empty-taloned. Horizontally, there is no doubt the swift can outfly the hawk.

At 8:10 there was a quick triple play of a tiny iridescent green hummingbird, *Chlorostilbon canivetii*, one of the emeralds, hardly more than two and a half inches overall. After its arrival, it passed in a matter of seconds from male to female to Bob, who flew off and made a crash landing among leaves but clung to his morsel. When he climbed into the open, having transferred the bird to his beak, he stood, chittered to the world and watched the horizon for three minutes before he partly plucked and devoured the little creature.

At 11:30 the female flew to her perch with a small, compact bundle which turned out to be the white-throated head of a Rancho Grande swallow. She must have plucked the bird, decapitated it, and given the rest to her young. At noon I happened to look at the nest and there was Nod with the rest of the swallow, working on it by herself.

May 16: Took glasses to room. Female flew to perch at 5:20 A.M., followed almost at once by the other three, Nod coming from nest. All flew about calling and perching now and then, then both settled on high branches and the parents vanished. At 5:35 female took a small bird from male. Bob flew up and clung partly to the female's perch. Only after a tussle would the female give up the bird, but finally Bob got it. It was *Chrysuronia oenone*. Soon the male brought a short-tailed swift, when neblina settled down and stopped observation.

At 1 P.M. the female herself caught a male *Volatinia jacarina* and after plucking and eating the head, gave it to Bob. He did not immediately eat it and his mother tried to get it back from him, whereupon he devoured it hastily.

May 19: (After two days in Caracas). Missed early catches but at 7 A.M. the female arrived with male *Sporophila nigricollis*, was attacked by Bob but shook him off in mid-air in no uncertain way and ate her bird in peace. After removing most of the feathers she ate every part, including head, wings,

legs and feet, then for some time she performed her picking dance on the stub.

At 7:30 female, Bob and Nod close together at the top of the candelo. The young are greenish-blue around the eyes and on the cere where the parents are bright yellow. They have not learned yet to face up wind, so their plumage often blows the wrong way. Also their stance is uncertain, and they still creep and crawl along a branch with help of waving wings. In flight they have good control and are strong, but alighting is still weak, and I have seen no attempt to learn to hunt.

The male brought a hummingbird at 8:20, a *Chrysuronia oenone*, and ate it. This seems to be the regular early morning routine, a bird to each young, or perhaps a bat, or a second bird, then one each eaten by the adults. There is often a second morning's period of activity, but little hunting in the middle of the day; a final season of hunting activity comes in the afternoon.

At 10 a vulture soared low over the candelo tree and the two falcons took after him at once, and alternately hit him again and again, driving him dodging into the valley. The youngsters followed behind their parents, screaming lustily. This day after day watching impresses me with the total lack of play or any alleviation of their routine. They arrive in early morning, watch for a time; dash off, kill, feed their young and themselves, perhaps repeat, and when all are fed they sit quietly for hours, forever looking about and preening, seldom sleeping. In late afternoon the activities are repeated, and sometimes before dark they vanish, going somewhere to sleep.

At 4:30 all four falcons were, for the first time, within the same field of view of the 20-powers. At 4:45 the male made two unsuccessful forays. The young got very impatient and bothered the female. Then both, on separate perches, began tearing at the surrounding leaves, making the bits of old airplant flower stalks and dead leaves fly, while Nod ripped up bits of loose bark and lichens. It was an interesting imitation of the adults.

May 20: After the first terrific rainstorm of the rainy season, at 12:30 saw Bob in nest eating the remains of a bat. He left and all four did much circling and chasing one another. At 4 o'clock all four joined in a renewed season of flight, diving at one another, and playfully striking with out-reaching talons. I was wrong in the matter of play practice. At 4:30 female caught a white-breasted martin. Yesterday I saw about forty of these birds passing down Limon Valley.

May 25: Twice the young birds have been seen to drop prey which had been given them or taken from the parents. The first time it was a blue-and-white swallow, which dropped and flew off apparently unhurt. The second time a female euphonia dropped headlong when the young lost its grip. Early morning and especially in late afternoon, just before the birds disappear for the night, the aerial evolutions continue. Several times I have seen the female, and once the male as well, literally brush or knock the young birds off their perch, and the young then pursue their parents at full speed. The favorite circling and pursuit area is near the Pass and down over the caciques' tree, the latter seeming to pay no attention.

May 27: Male on perch at 5:15, others soon after. Nod swooped down for a brief visit to her nest, perching on the rim for five minutes. A bat at 6:10 from male to female to Bob, a small species with small, rounded ears. She had trouble with the wings. A bird at 6:55, male to female to Nod, who took it to a special perch of her own. This was a jacamar, *Galbula ruficauda*, the first of its kind. The wing and tail feathers came out easily, but she could do nothing with the head or long beak and ate only what she could detach. At 7:15 male dined alone on a *Adelomyias melanogenys*, the first of this species to enter into the falcon's diet.

May 29: Late afternoon notes: 4:45, both adults left for the night. At 5 both young flew in large circles, over Rancho Grande down south and back, occasionally closing wings and making a little swoop. Returned, perched close together, and yelled in concert. Bob vanished. Nod returned from a short flight with something in her claws, which she dropped in mid-air, a yellow butterfly, *Phoebis eubule*. It seems to have been her first catch.

Later, adults appeared unexpectedly. Sat for a while, then they went for good. Bob flew into the heart of candelo number two, and Nod flew down for a night in the nest.

May 30: This morning got the clue to the beginning of hunt learning. They were both knocked off their perches and followed and struck repeatedly at one or the other of their parents. Then Bob circled and again and again dived and struck at some small insect, never getting it. Then repeated twice, and both youngsters did it. A large yellow leaf fell from the candelo and Nod swooped after it but missed. Yesterday she had been more successful with the pierid butterfly. This seems the transition from flight learning to the first attack. It would seem that the final finished lethal swoop must be many weeks away.

May 31: All four at 5:30. Adults left almost at once, young made a few circling flights. At 6:15 male returned with prey which Bob snatched and took behind a limb. Although I could not see it I knew it was a bat, for throughout the plucking in a fair wind, not a feather drifted away. Later Nod perched below her father and yelled continuously until he left. Then she swooped and chased a swallow in front of Rancho Grande, missing it by a mile, more or less! Her first attempt on a real bird as far as my observations went.

June 5: (After return from Caracas). At 11:54 three falcons in the same candelo, the male, Nod and Bob. Nod was holding a short-tailed swift and plucking it. Bob was watch-

ing with only casual interest so he must have already fed. Two primary feathers soon dropped and drifted away in the breeze. Bob made a feint after them and finally swooped and came back with both in his beak. He toyed with them, let them drop. Soon he repeated his capture with another feather and still another. In this way was skill attained.

June 6: At 8:15 and again at 10 I was at the Pass, watching with amazement as flock after flock of sharp-tailed manakins, *Chiroxiphia lanceolata*, went past overhead, from south to north, 8 to 26 in each group. These are rather solitary residents of lowland jungle and this was an unexpected minor migration. Between these times I was behind my glasses in the laboratory and at 9:15 I saw the female falcon holding and slowly plucking one of these beautiful birds. The tousled scarlet, blue and black was then given to Nod. In this case, as in many others, the falcons drew upon the regular or irregular migration through the Pass.

June 10: At 1:30 a swallow-tailed kite appeared and the female falcon took after him, later joined by the male. They swooped with terrific speed, but the kite simply side-rolled, with effortless but lightning-like countering movements, and the falcons shot past and never hit. He rose a hundred feet and then returned, seeming to enjoy the conflict, giving a sense of reserve strength and speed which put the utmost efforts of the past masters of the air—the falcons—to naught. Never have I seen such different, and such perfection of, aerial evolutions. While the kite seemed merely to be egging on the small birds, they were in deadly earnest, wasting much energy in loud chittering. When he desired, he rose in a spiral, losing only a few feet at each counter, and vanished through the Pass.

The daily pursuit in mid-air of young and old falcons goes on steadily, morning and late afternoon for many minutes. It is definitely a method of practice.

June 11: After flight evolutions Nod was traced to a stub above the nest. She flew down and dug or scraped about on the floor for a long time. Male later brought a fork-tailed swift, *Panyptila cayennensis*.

June 12: 8:15 Bob nowhere in sight. Nod quiet on top perch. Male brought bird, female began half-heartedly to pluck, held in it beak, then called loudly. The bird is a male golden siskin, *Spinus psaltria*. Female dived with it to nest, entered, waited, called loudly, stood on rim and left. She carried the prey up to a horizontal branch and cached it among some airplant leaves.

June 13: At 6 A.M. female arrived with bird and was mobbed by both young. Bob followed her to perch and almost knocked her off and got the prey. I followed him to his own perch, where he spent much time calling and bobbing and looking around before he began plucking. I first saw the spiny tail, then the long, curved wings, then the head and knew it was another of the rare white-spotted swifts, *Cypseloides cherriei*, the ninth specimen seen by us at Rancho Grande and the twelfth known to ornithology.

June 17: The young arrive before the old birds these mornings, and chitter till their parents appear. Then more calling until the birds start off hunting. Nod appeared with a long, thin object, and found she was carrying a good-sized stick, a half-inch through and four long. She circled again and again, dragging it with her, and finally tried to alight, and got it stuck with her own wing over a branch, finally having to let the wood go. But she retrieved it before it struck the earth in the best performance I have seen. Carrying it to a higher perch, she savagely bit off pieces of rotten chips.

June 19: For two days Nod has been left alone by the other three birds, spending much of the time on a top branch calling. At 10:15 she was tearing apart a white-breasted swift, *Aeronautes montivagus*. Two hours before I had seen six of these birds rushing south through the Pass, and suppose that the falcon's prey was one of these unusual migrants. Other individuals of this swift were taken on April 4 and June 19.

June 22: The morning activities are now shaping into a new and final pattern. At 5:30 A.M. Nod arrived on her perch. For 45 minutes she called and did her hunger dance. At 6:15 the female swooped up, called, looked at her offspring and streaked for Limon Valley. Until 9 Nod waited and called. Then she flew down to the nest and lighted on the rim. This seems an unusual thing for a hawk to do. Forty-one days ago she left the nest and now she returned and the rolling neblina hid her from my view. Bob appeared at noon for a few minutes. Nod alone until she left at 6:15 P.M.

June 23: Nod on perch at 6. The other three soon arrived and left. Nod did her dance, frantically picking at the lichens, patting with her feet and revolving on her stub. At 11 female returned with a hummingbird, a *Chrysuronia oenone*. Bob returned at noon, apparently well fed, for he paid no attention to his sister who, having disposed of the hummer, was now happy with a bat.

June 26: Female brought a short-tailed swift. Nod met her in mid-air, took it and promptly dropped it. The female swooped but was too late to retrieve it before it reached the jungle foliage. Came back and chittered, with what sounded to my human mind appropriate sentiments, and left. When Bob came Nod chittered to him and begged as if from a parent.

June 28: Nod at 5:30. Flew about and occasionally hesitated and shifted with outstretched claws as if reaching for some invisible prey. No parents, and soon neblina enveloped her. Just at dusk, as I was passing, I saw fresh lime on the nest rim.

June 29: Nod flying in early morning in large circles, now and then striking at something, but as far as I could see, getting nothing. On her next flight she slowed up abruptly and struck at what looked like a small bat. She seized and took it to her perch. As I

focussed, she tumbled off and perched on a lower branch. She held a full-sized male hercules beetle, *Dynastes hercules*. The elytra of the great insect seemed to have closed down over one of her toes, and she had trouble tearing it away. The elytra and the flying wings were then torn off and the body was eaten.

June 30: Nod flew up from the direction of the nest at 5:55. After I had finished breakfast I saw she had a small bat and the female falcon was just leaving for the valley.

July 3: At 11 Nod left her perch and swooped down close to where I stood in the road, and clutched something in the top foliage of a tree. She emerged with a giant, red-winged grasshopper, *Tropidacris dux*, which fluttered as he was being carried. Finally he freed himself, but Nod swooped and caught him fairly in mid-air, and ate all but the wings.

The routine now is, Nod sleeps near or in the nest, and perches early. Bob and the parents appear later than before, sometimes coming for an hour around mid-day. The female still feeds Nod but irregularly. She is usually alone in late afternoon and leaves about 6 P.M.

July 5: 9:15. Both young birds mobbed the female when she appeared, although she had no food. For most of the morning they hawked after insects. One caught a big yellow butterfly, *Phoebis eubule*, and Nod flew after but missed two others. The birds are far from skilful but are eking out their reduced rations with insects.

July 8: At 10, fairly heavy neblina and chilly. The young birds hunted insects, once swooping over Rancho Grande and sending every swallow, old and young, into the rooms. When the old falcons are not around, the swallows seem to pay little attention to the young birds, very distinctly seeming to gauge their ineffectiveness in the air. Bob appeared and with Nod made twelve attacks on a lone yellow butterfly, but it flicked aside every time. As entomologists the young hawks use up a tremendous amount of energy for very small pickings.

At 10 the female came to the tree with a chestnut-collared swift and Bob seized it. Before it was devoured, neblina closed in and the rain came down in torrents. At 12:15 the weather had cleared and Nod was soon perched with a prize. She had caught herself a giant, white-striped nymphalid butterfly, *Victorina epaphus*. A few minutes before, we had seen four and twenty of these butterflies flying south through the Pass. At her first peck the wings hung down in full view, then they fluttered away to earth, and the hawk ate every particle of the insect and picked at the stub splinters afterward. Later, when all four falcons were perched on their lofty perches, a rufous-tailed squirrel naively came and looked into the nest. He would probably have been perfectly safe; much too large and heavy even for the valiant falcons.

July 9: Male and female at 5:45 and both went through their dance. At 6 Nod caught a sphinx moth at the first attempt, and ate it. It was a green *Xylophanes*, species not recognied. At 7:15 Bob dashed into a mass of treetop leaves and emerged with an eighteen-inch slender greenish snake in his claws. Probably the common *Herpetodryas carinatus*. He half lost the reptile, got a fresh hold, and when the serpent twisted upward lost it for good, and it fell still writhing into Limon Valley. At 12:30 Bob and Nod sailing around together. Bob dived at a passing insect, caught it, and in mid-air transferred it from claws to beak. Saw its knobbed antennae and coiling tongue and then the wings of a papilio. Fleming looked and identified it as one of the tailless aristolochia group, *Papilio arcas arcas*, a male. He had just taken one at kilometer 31, and I had seen it at the Pass this very morning. Bob pinched off one green and black forewing, which I watched as it fluttered slowly down to the very jungle floor. Then the scarlet and black hindwings dangled and showed every detail. She nibbled at the body and then discarded it, after all her work. This very likely reflects the supposedly inedible, bitter quality of the body juices of this group of butterflies.

Both birds launched out and Nod returned with a sizeable green leaf, and did her dance, pretending to bite at the leaf as she held it in her claws. Rain started straight down and both took a real bath, spreading wings and tail to full extent and revolving on their tiny perches. It was the first real relaxation I have observed in the family.

July 11: At 9:45 Nod suddenly swooped down to the nest and spent twenty minutes there, scuffling around the bottom, pecking and gazing from the edge at nothing in particular. The increased lime marks on the rim make it certain that she must sleep there. Today is only two days less than two full months since she left.

July 12: Much rain and neblina so I missed the hunting and feeding. At 8:45 Nod dived after and caught a yellow leaf and devoted much energy to its destruction. At noon, female came with bat, was mobbed by both young. All were absolutely soaked but Nod won out and would not give up the prey.

July 14: At 10:30 we left the Pass and soon afterwards onrushing, low neblina sent the migrating butterflies high into the air and the young falcons had an exciting time. Bob dived twice at a dark butterfly which turned out to be a *Victorina*. Bob chased the butterfly and Nod chased Bob, but at last Bob found a safe perch and ate his prey. Nod went to the nest, climbed up on one side, then swooped out and caught a dark nymphalid and ate it quickly. A single glimpse of the under wings identified it as *Marpesia coresia*. Then out again and flushed a large caligo from a tree, *Caligo eurilochus*. The great owl butterfly rose swiftly and darted irregularly upward, but at her first down swoop Nod got it. She carried it to the nest and one huge wing fell to the bottom as she ate the insect.

At 12:15 Bob got a small hummingbird

which his mother brought him, and devoured every bit. It was *Chlorostilbon aliciae.*

I tried to locate Nod's *ke-ke-ke* on the scale, and it proved to be the note B, two octaves above middle C, much higher than one would think.

The long, dangling bunched masses of orchids almost overhanging the nest of the falcons have never fruited, although they have blossomed. This is doubtless due to their never having been visited by hummingbirds, for obvious reasons, and therefore have never been fertilized. The orchid is *Elleanthus* species? (Department Tropical Research, Bot. Cat. No. 140). Similar plants and flowers on the neighboring trees have all fruited.

July 18: For the first time in the history of the family, no falcon in sight all day, not even Nod.

July 19: Nod on perch early. Bob at 6:15, both soon leaving.

July 23: Bob on perch at 6, and saw Nod leave the nest to join him.

July 27: More and more the three hawks are away and Nod is alone, but occasionally fed by the female. She sleeps every night in the nest, and early this morning, after a long downpour in the night, I saw Nod on the rim and Bob behind her, both with dry plumage, so they must both have spent the night there.

July 29: At 4 P.M. a very severe electrical storm, and Nod appeared and flew to the nest where she looked out at the bad weather in perfect shelter. Either this behavior is a sign of weakness and inability to face the elements, or it may represent an advance on Bob, an ability to utilize shelter and thus husband energy. All depends on whether Bob has outgrown her in expert foraging for himself. At dark she was still crouched in the nest.

July 31: Nod on perch alone in morning. At dusk Nod in the nest.

August 1: Early this morning Nod caught and brought to her perch a hummingbird, *Chrysuronia oenone*, and ate it. As far as I know this was her first vertebrate prey caught alive.

At 10 A.M. we left Rancho Grande, so this is the last note made on the life history of *Falco albigularis.*

SYSTEMATIC LIST OF OBSERVED PREY AND THE NUMBERS OF INDIVIDUALS CAPTURED BY *Falco albigularis albigularis.*

Species represent certain sight identifications; subspecies are based on geographical expectancies.

**Mammals — 33**

*Heteromys anomalus* (Jungle mouse) — 1
*Carollia perspicillatum* (Dog-faced bat) — 4
*Chilonycteris rubiginosa* (Large orange bat) — 3
*Lonchoglossa caudifera* (Common culvert bat) — 23
*Uroderma bilobatum* (White-lined bat) — 2

**Birds — 163**

Apodidae — 26
*Streptoprocne zonaris albicincta* — 3
*Chaetura cinereiventris lawrencei* — 1
*Chaetura brachyura brachyura* — 12
*Chaetura rutila brunneitorques* — 3
*Cypseloides cryptus* — 1
*Cypseloides cherriei* — 2
*Aeronautes montivagus montivagus* — 3
*Panyptila cayennensis* — 1

Trochilidae — 34
*Phaethornis augusti augusti* — 1
*Anthracothorax nigricollis nigricollis* — 2 (males)
*Chlorostilbon canivetii caribaeus* — 3
*Chlorostilbon aliciae* — 3
*Chrysuronia oenone oenone* — 9
*Chalybura buffonii aeneicauda* — 2
*Adelomyias melanogenys aeneosticta* — 1
*Ochreatus underwoodii polystictus* — 7 (6 males)
*Aglaiocercus kingi margarethae* — 5 (4 males)
*Chaetocercus jourdanii rosae* — 1

Galbulidae — 1
*Galbula ruficauda ruficauda* — 1

Pipridae — 1
*Chiroxiphia lanceolata* — 1

Tyrannidae — 6
*Fluvicola pica pica* — 3
*Pyrocephalus rubinus saturatus* — 1
*Myiozetetes cayennensis rufipennis* — 2

Hirundinidae—17
*Progne chalybea chalybea* — 4
*Stelgidopteryx ruficollis aequalis* — 2
*Pygochelidon cyanoleuca cyanoleuca* — 7
*Hirundo rustica erythrogaster* — 2
*Iridoprocne albiventer* — 2

Mimidae — 1
*Mimus gilvus melanopterus* — 1

Sylviidae — 2
*Polioptila plumbea plumbiceps* — 2

Vireonidae — 1
*Vireo olivaceus vividior* — 1

Coerebidae — 5
*Chlorophanes spiza spiza* — 1
*Coereba flaveola luteola* — 4

Parulidae — 10
*Compsothlypis pitiayumi* — 1
*Dendroica striata* — 1
*Setophaga ruticilla ruticilla* — 5
*Basileuterus tristriatus meridanus* — 1
*Basileuterus culicivorus cabanisi* — 2

Icteridae — 1
*Icterus chrysaetus giraudii* — 1

Tersinidae — 1
*Tersina viridis occidentalis* — 1

Thraupidae — 19
*Tanagra musica intermedia* — 2
*Tanagra xanthogaster exsul* — 1
*Tanagra trinitatis* — 1
*Tanagra laniirostris crassirostris* — 2 (males)

*Tanagra* females sp? — 3
*Tangara chrysophrys chrysophrys* — 1
*Tangara arthus arthus* — 3
*Tangara gyrola toddi* — 2
*Compsocoma flavinucha venezuelana* — 1
*Thraupis virens cana* — 1
*Chlorospingus ophthalmicus jacqueti* — 2

Fringillidae — 12
*Pheucticus chrysopeplus laubmanni* — 1
*Tiaris bicolor omissa* — 1
*Sporophila nigricollis nigricollis* — 5 (males)
*Volatinia jacarina splendens* — 2 (males)
*Spinus psaltria colombianus* — 2
*Sicalis flaveola flaveola* — 1

Unidentified birds — 26

**Reptiles — 2**
*Anolis squamulosus* — 1
*Herpetodryas carinatus* — 1

**Amphibia — 1**
*Gastrotheca ovifera* — 1

**Insects — 19**

Lepidoptera
*Marpesia coresia* — 1
*Phoebis eubule* — 5
*Victorina epaphus* — 2
*Papilio arcas arcas* — 1 (male)
*Morpho peleides corydon* — 1
*Caligo eurilochus caesia* — 1
Unidentified butterflies — 3
*Pholus obliquus* — 1
*Xylophanes* species — 1

Orthoptera
*Tropidacris dux* — 1

Homoptera
*Cicada* species — 1

Coleoptera
*Dynastes hercules* — 1

### General Summary.

Taking into consideration the many days away from observation, and the intermittent hours which we were able to devote to watching, a conservative estimate of individual prey captured by the bat falcons during the five and a half months would be not less than 600 birds and bats.

The total recorded is as follows:

| | *Species* | *Individuals* |
|---|---|---|
| Mammals | 5 | 33 |
| Birds | 56 | 163 |
| Reptiles | 2 | 2 |
| Amphibia | 1 | 1 |
| Insects | 14 | 19 |
| | 78 | 218 |

The proportion of essentially aerial forms is as follows: bats 4 species, 32 individuals; swifts 8 and 26; hummingbirds 10 and 34; swallows 5 and 17; lepidoptera 11 species and 16 individuals. This totals 38 and 125, which thus comprise respectively 50 per cent. of all the species, and 57 per cent. of all the individuals. These figures of essential flyers do not include such aerial-feeding birds as galbula and flycatchers.

Another interesting fact is the large number of lowland forms in the diet. Some of these may have been taken as they migrated through Portachuelo Pass, but the majority must have been transported several kilometers from the relatively low country about Limon and Maracay. There is no doubt but that the majority of the prey was captured at a considerable distance from the nest.

Concerning avian prey alone, we can make the following distinctions, in regard to four phases of habitat:

| | *Species* | *Specimens* |
|---|---|---|
| Aerial | 23 | 87 |
| Tree-tops | 19 | 37 |
| Open country | 10 | 17 |
| Jungle | 4 | 5 |

A moment's consideration shows the reasonableness of the respective divisions and their relative numbers. We are dealing with predators whose method of hunting is by keenness of vision, with stance on a lofty, exposed perch, and an ultimate dive from a still greater height, plummeting at full speed upon the victim.

This explains the relative proportions of these subdivisions, the preponderance of aerial and tree-top species and numbers, the fewer number of open country, savanna and grass-inhabiting forms, and the disproportionately small percentage of prey living in the heart of dense jungle.

# 5.

# The Vampyromorpha (Cephalopoda) of the Bermuda Oceanographic Expeditions.[1]

GRACE E. PICKFORD.
*Bingham Oceanographic Laboratory, Yale University.*

(Text-figures 1-8).

## INTRODUCTION.

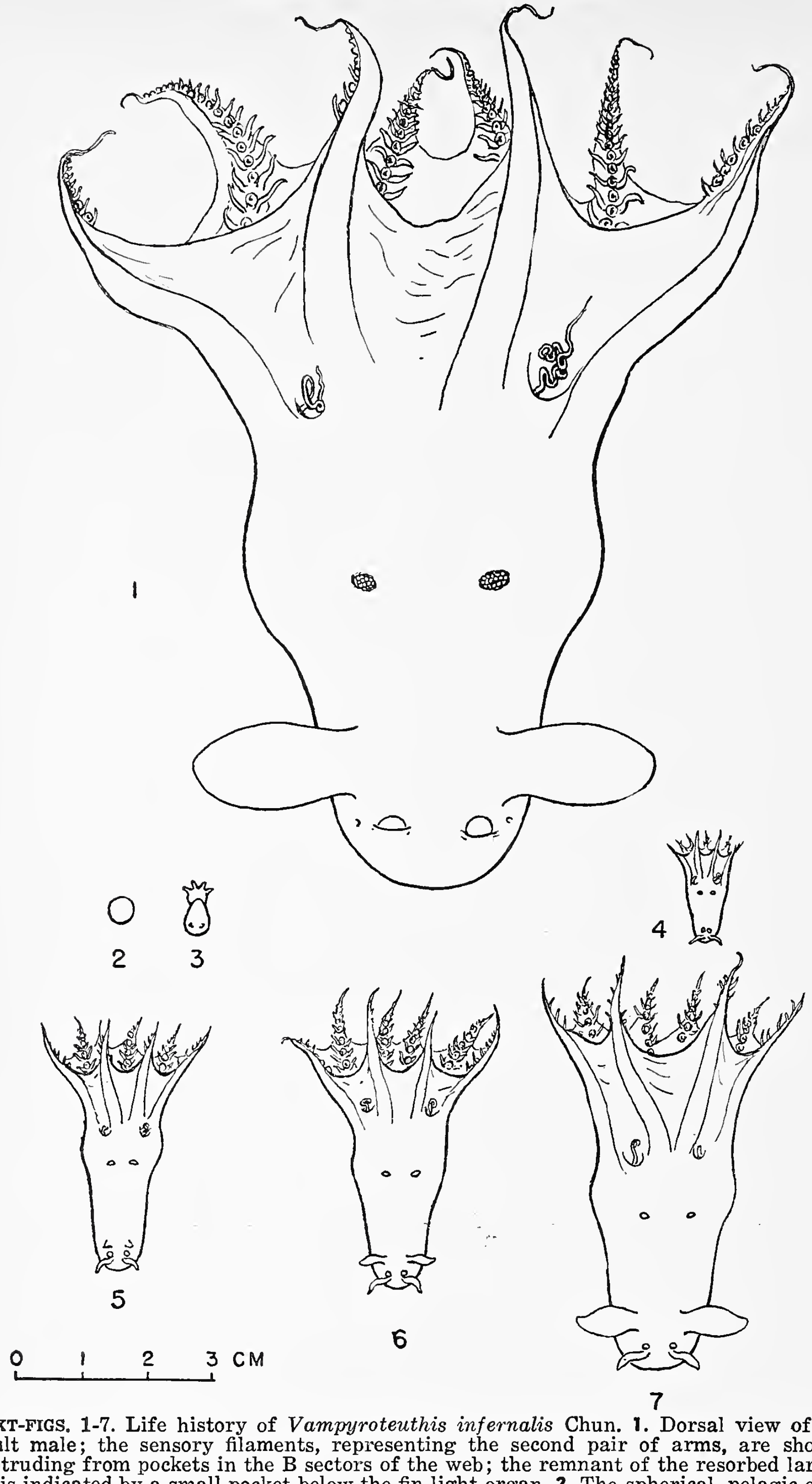
It was the good fortune of the Bermuda Oceanographic Expeditions of the New York Zoological Society, under the direction of Dr. William Beebe, to capture no less than eighteen specimens of the rather rare, bathypelagic cephalopod, *Vampyroteuthis infernalis* Chun. The addition of this new material augments the number of recorded specimens to 95, 59 of which are from the Atlantic. Moreover, Dr. Beebe's specimens, which are all larvae, constitute the largest series that has ever been taken at a single station, within so small and narrowly restricted a geographical area. Furthermore they are the only specimens ever collected for which the depth of capture is rather accurately known, having been checked with the aid of a bathygraph and not merely estimated from the length of the towline. Their capture in the Bermuda area extends the northern distribution of this species in the western Atlantic by about 8° of latitude, the nearest previous records being those of the *Pawnee* and of the *Atlantis*, somewhat to the south of this region. The comparative rarity of this animal is attested by the fact that it was taken by this expedition on only 18 occasions out of a total of more than 800 hauls at suitable depths. The collection provides a valuable opportunity for the confirmation, or rejection, of certain conclusions drawn from previous records and representing a total of 75 specimens taken from scattered stations in many different parts of the world. The present contribution is designed to lay special emphasis on this aspect of the problem.

The conditions under which the collections were made have been described by Beebe (1931a) and were summarized as follows by Coe (1945): "The collections were all made by Dr. William Beebe in a relatively minute portion of the deep subtropical Atlantic Ocean. This portion was a circular column of water eight miles in diameter, with its center located at 32° 12′ N. Lat., 64° 36′ W. Long., about nine miles southeast of Nonsuch Island, Bermuda. The nets were drawn horizontally across this area so as to collect samples simultaneously at 200-meter intervals from depths of about 1,000 to 2,000 meters. During the years 1929, 1930 and 1931 a total of 1,042 nets one meter in diameter were drawn at these depths in all directions across this eight-mile cylinder of water."

It may be useful, for the benefit of readers not already familiar with the story, to summarize some of the more interesting features in our knowledge of this remarkable animal. The biology and external morphology have been the subject of an extensive investigation, the results of which are published in the *Dana* Reports (Pickford, 1946 and 1949a). The internal anatomy, which is still under investigation, has been treated more briefly (Pickford, 1939b and 1940). *Vampyroteuthis infernalis* is an aberrant, but in many respects rather primitive and archaic dibranchiate cephalopod. It has ten pairs of arms, but the second pair is modified to form slender, sensory filaments which may be retracted into pockets on the aboral surface of the web. For this reason it cannot be placed either with the Decapoda, in which the fourth pair of arms are modified as tentacles, or with the Octopoda, which possess only eight pairs of arms. The order, or suborder Vampyromorpha Robson (emend.), to which it is assigned, thus represents a third group of dibranchiate cephalopods related, by the form of the gladius, to the extinct Prototeuthoidea.

The adult animal attains a mantle-length of 50 mm. in males, and perhaps 80 mm. in females. The head-width is nearly as great as mantle-length and the web is extensive (Text-fig. 1). The arms, like those of the Cirromorpha, bear a single row of suckers that alternate with pairs of cirri. A certain number of cirrus-pairs, the primary cirri, precede the first sucker on each arm. The external surface of the body is jet black, except for the oral face of the web which is red-brown. Near the apex of the body there is a pair of paddle-shaped fins. Just behind the base of each fin there is a circular luminous organ which may be occluded by an eyelid; on the back of the neck there are two clusters of luminous nodules and almost the whole external surface of the animal, except the oral face of the web, is decorated with minute, simple light organs.

[1] Contribution No. 873, Department of Tropical Research, New York Zoological Society.




TEXT-FIGS. 1-7. Life history of *Vampyroteuthis infernalis* Chun. **1.** Dorsal view of an adult male; the sensory filaments, representing the second pair of arms, are shown protruding from pockets in the B sectors of the web; the remnant of the resorbed larval fin is indicated by a small pocket below the fin light organ. **2.** The spherical, pelagic egg. **3.** A post-embryo; dorsal view of the youngest known specimen showing one pair of larval fins, and the squid-like, anteriorly projecting mantle margin. **4.** A typical stage 1 larva. **5.** An early stage 2 larva, showing anterior fin rudiments in front of the fin light organs. **6.** A typical four-finned, stage 3 larva. **7.** A stage 4 larva showing the animal as it appears somewhat previous to the resorption of the larval fins. All drawings to the same scale. Drawings by Lisbeth Krause.

The life history of *Vampyroteuthis* is most interesting since it undergoes what may be described as a double metamorphosis. The eggs (Pickford, 1949b) are about 3.86 mm. in diameter, spherical, and pelagic. The youngest larva ever captured (Text-fig. 3) has a mantle-length of 5.5 mm. and is provided with a slender pair of larval fins that are set diagonally so that it appears probable that the animal must swim head downwards like other larval cephalopods. A most interesting feature of this youngest stage is the forwardly projecting, squid-like, dorsal mantle-margin. In older larvae and in adults this becomes sunk within the enveloping, subcutaneous gelatinous tissue so that the animal assumes a superficial resemblance to the Octopoda.

The distinctive nature of the larval fin becomes apparent in slightly older larvae (Text-fig. 4) in which the fin light organ is developed and is found to be situated *in front* of the fin base, not behind it as in adults. At a mantle-length of about 10 mm. one can find a minute anterior fin rudiment, situated in front of the fin light organ (Text-fig. 5). The appearance of this rudiment inaugurates the second larval stage. The future adult fin grows rapidly and becomes paddle-shaped, while the length of the larval fin increases but little if at all. When the two fins are subequal, at an average mantle-length of 18 mm., the animal is considered to be in the third, or typical four-finned larval stage (Text-fig. 6). As growth proceeds the anterior fin becomes progressively larger and soon greatly exceeds the length of the larval fin; this is the fourth and last larval stage (Text-fig. 7). At a mantle-length of between 25 and 30 mm. the larval fin, whose length has scarcely changed since it became established in the 10 mm. larva, undergoes a sudden resorption. This constitutes the definitive and final metamorphosis of the larva into the adult form (stage 5) and is accompanied by many changes in the growth relationships of the bodily parts. A minute vestige of the larval fin can be found in adult animals, in the form of a little pocket situated just behind the fin light organ.

*Vampyroteuthis infernalis* is found in the Deep Water of all tropical and subtropical oceans. It has rarely been taken at estimated depths of less than 1,000 meters and is certainly absent from the upper 300 meters of the ocean. It is stenothermic and stenohaline and is commonly found just under the oxygen minimum, in water of density represented by $\sigma t$ 27.6 to 27.8. The idea that it may be restricted to a constant density layer, which was suggested to me by Dr. E. F. Thompson, appears to be confirmed by a comparison of the vertical distribution in the different oceans. Specimens from the Indo-Pacific have usually been taken at greater depths than those from the Atlantic, in water that is colder and less saline but whose density is the same as that of the layer of maximum abundance in the Atlantic. As far as is known, the eggs are also restricted to this density layer.

It seems to be quite certain that there is only one species of *Vampyroteuthis*. Previous descriptions by earlier investigators, who recognised as many as eleven species distributed among eight supposedly different genera, were based upon distorted and abnormally preserved specimens, and upon ignorance of the life history. An exhaustive study of the external characters has shown that there are no differences of a specific or even of a subspecific nature between the populations of the three great oceans. Yet there is reason to believe that the Atlantic population constitutes a distinct race, separable from the Indo-Pacific group by the average number of pairs of primary cirri on the arms. Dr. Beebe's collection of 18 specimens provides an admirable opportunity to examine this hypothesis which, it may be mentioned in anticipation, appears to receive adequate confirmation.

It is a pleasure to acknowledge my thanks to Dr. William Beebe for the privilege of examining this important and interesting series of specimens, to Dr. Gordan A. Riley for assistance with the hydrographic data, to Miss Lisbeth Krause for the drawings of the life history (Text-figs. 1-7), and to Dr. Daniel Merriman, Director of the Bingham Oceanographic Laboratory, for his continued interest in my investigations.

## Seasonal Distribution, Vertical Distribution, and Hydrographic Correlations.

The specimens captured by the Bermuda Oceanographic Expeditions are listed in Table I which gives the date, net type and depth. In the last column I have given the length of the towline, obtained by doubling the estimated depth. In regard to the latter, Dr. Beebe states (in litt.) that "The bathygraph was used only occasionally to verify our estimates as to the depth of the trawling net. We found that at a speed of 2 knots and an angle of 30 degrees, the tests with the bathygraph agreed perfectly with our estimate of the depth as one-half of the amount of cable out." It is most satisfactory to have this confirmation of the estimated depth of capture, enhancing, as it does, the validity of the hydrographic interpretations which, for all other expeditions, have been based upon arbitrary assumptions.

*Seasonal distribution.* Previous investigations have indicated that larval vampyromorphs might be taken at all seasons, but the data were quite inadequate for a study of relative abundance. The Bermuda collections were made during the summer months, from April to October, but a tabulation of the data (Table II) indicates a period of maximum abundance in this region during June and July. The depths are tabulated but provide no evidence of vertical migration and the total numbers at all depths may therefore be considered. Comparatively few hauls at suitable depths were made in April

TABLE I.

List of Specimens.

| No.[1] | Net No.[2] | Date | Net type | Depth meters | Towline meters[3] |
|---|---|---|---|---|---|
| 78 | 331 | VII.27.1929 | 1 metre | 1,829 | 3,658 |
| 79 | 700 | VI.13.1930 | 1 metre | 1,463 | 2,926 |
| 80 | 807 | VII.16.1930 | 1 metre | 1,463 | 2,926 |
| 81 | 800 | VII.15.1930 | 1 metre | 1,463 | 2,926 |
| 82 | 710 | VI.16.1930 | 1 metre | 1,280 | 2,560 |
| 83 | 668 | VI.4.1930 | 1 metre | 1,463 | 2,926 |
| 84 | 861 | IX.8.1930 | 1 metre | 1,280 | 2,560 |
| 85 | 328 | VII.27.1929 | 1 metre | 1,463 | 2,926 |
| 86 | 731 | VI.27.1930 | 1 metre | 1,463 | 2,926 |
| 87 | 785 | VII.7.1930 | 1 metre | 1,097 | 2,194 |
| 88 | 280 | VII.10.1929 | 1 metre | 1,280 | 2,560 |
| 89 | 25 | IV.15.1929 | 1 metre | 1,463 | 2,926 |
| 90 | 788 | VII.7.1930 | 1 metre | 1,646 | 3,292 |
| 91 | 1229 | VIII.27.1931 | 1 metre | 1,463 | 2,926 |
| 92 | 724 | VI.25.1930 | 1 metre | 1,829 | 3,658 |
| 93 | 455 | IX.10.1929 | 1 metre | 1,829 | 3,658 |
| 94 | 76 | V.8.1929 | 1 metre | 1,463 | 2,926 |
| 95 | 198 | VI.20.1929 | 2 metre | 1,829 | 3,658 |

1 Author's register of known specimens; Nos. 1-77 are listed in the *Dana* Reports (Pickford, 1946 and 1949a).
2 Data from the published Station Lists (Beebe, 1931b, and 1932).
3 Twice the estimated depth of capture (see text).

and the paucity of *Vampyroteuthis* at this time is, therefore, of uncertain significance. The same is not true in May when a total of 114 hauls captured only one animal. In June and July, with 186 and 146 hauls respectively, a total of 13 specimens was taken. In August, as in May, an equally extensive series of hauls captured only one specimen. The data for September are even more significant; nearly twice as many nets were lowered as in July and yet only two vampyromorphs were taken. In October, as in April, too few hauls were made to permit interpretation of the negative results.

Two interpretations are possible, either the larvae are more abundant in June and July, or they migrate into the Bermuda region at this season. The latter hypothesis receives support from two sources. Larval vampyromorphs have been taken from other parts of the Atlantic at all times of year and the otherwise rather inexplicable absence of even young adults from the Bermuda collections might be explained along these lines since there is some evidence that the larvae range more widely than the adults. However, the absence of larger specimens might be due to the fact that most of the towings were made with one-meter nets. The rich collections of the *Dana* Expeditions were made, for the most part, with two- and three-meter nets.

*Vertical distribution.* No specimens were taken at depths of less than 1,000 meters. This fact is significant since a total of 469 nets was lowered at depths ranging from 0-914 meters; 172 of these were at 914 meters and if *Vampyroteuthis* occurred at this depth it seems probable that at least one or two specimens would have been taken. As a matter of fact only one specimen was taken above 1,200 meters, the majority being between 1,280 and 1,829 meters (Table II). The absence of specimens at depths of more than 2,000 meters cannot be interpreted on account of the small number of hauls, but in any case such towings must have been taken in close proximity to the bottom and the concensus of previous data suggests that *Vampyroteuthis* is not commonly taken within 250 meters of the bottom.

In order to compare the vertical distri-

TABLE II.

Summary of Data on Seasonal Distribution.

| Depth meters | Number of specimens | | | | | | | Total nets by depth |
|---|---|---|---|---|---|---|---|---|
| | Apr. | May | June | July | Aug. | Sept. | Oct. | |
| 1,097 | — | — | — | 1 | — | — | — | 175 |
| 1,280 | — | — | 1 | 1 | — | 1 | — | 172 |
| 1,463 | 1 | 1 | 3 | 3 | 1 | — | — | 174 |
| 1,643 | — | — | — | 1 | — | — | — | 174 |
| 1,829 | — | — | 1 | 2 | — | 1 | — | 178 |
| 2,011-3,640 | — | — | — | — | — | — | — | 10 |
| Total spec. | 1 | 1 | 5 | 8 | 1 | 2 | — | |
| Total nets by month | 33 | 114 | 184 | 146 | 137 | 259 | 10 | 883 |

TABLE III.

Summary of Data on Vertical Distribution.

| Group | Towline, in meters: 1,000-1,999 | 2,000-2,999 | 3,000-3,999 | 4,000 and over |
|---|---|---|---|---|
| Bermuda | — | 13 | 5 | — |
| Previous Atlantic records | 3 | 15 | 10 | 7 |
| Atlantic *Total* | 3 | 28 | 15 | 7 |
| Indo-Pacific *Total* | 1 | 5 | 12 | 14 |

bution of the Bermuda collection with that of previously recorded specimens it is convenient to present the data in terms of the length of the towline (Table III). The results show that the majority of specimens was taken with towlines of between 2,000 and 3,000 meters, in good agreement with previously published records from the Atlantic and in striking contrast to the Indo-Pacific in which the majority of specimens has been taken at greater depths. However, it must be remembered that, on account of the proximity of the bottom, few towings could be made with cable lengths of more than 4,000 meters and the absence of this species at greater depths, in suitable regions, is not therefore confirmed by the Bermuda collections.

*Hydrographic correlations.* It will be seen from Table IV that the majority of specimens came from 1,500 meters, in water of temperature of about 4.2 °C., 35.0 ‰ salinity, and density 27.8 $\sigma t$. This information is in admirable agreement with previous estimates for Atlantic specimens, the majority having been taken in water ranging from 3.0 to 6.0 °C., 34.9 to 35.0 ‰ salinity, and $\sigma t$ 27.6 to 27.8. The results are represented graphically in Text-fig. 8, in which the Bermuda water from which the 18 new specimens were captured is represented by a stippled rectangle. The possibility that the species may occur, in this region, in water of greater density cannot be excluded, for reasons explained under the paragraph dealing with vertical distribution but, on the other hand, it appears almost certain that it does not occur in layers of density less than $\sigma t$ 27.6. On the whole, the hypothesis that this species is rather narrowly restricted in its density distribution appears to receive considerable support.

It may be noted that the Bermuda specimens inhabited water that was rather well supplied with oxygen, so that the hypothesis that the species is rather oligoaerobic, although apparently supported by previous investigations, requires further confirmation.

## Morphological Characters.

Measurements were restricted to mantle-length, head-width and fin-length, since it appears that there is little further to be learned from a detailed study of other external proportions. The results are given in Table V. Twelve specimens are in the second larval stage, i.e., the adult fin is present but does not exceed 60% of the length of the larval fin. Two of these 12 specimens have only a minute bud representing the anterior fin rudiment and, if they had been less well preserved, this bud might easily have been overlooked. It is probable that such a rudiment is always present in larvae of mantle-length 9 to 10 mm. and that some of the specimens previously referred to stage 1 may really have been in this transitional condition, the fin rudiment having been lost through rubbing of the skin. Four more specimens have a well developed, triangular anterior fin bud. Two specimens, Nos. 81 and 88, are of special interest; the anterior fin is only about 0.5 mm. long but has already begun to elongate and passed beyond the condition of a triangular rudiment. The

TABLE IV.

Summary of Hydrographic Data.[1]

| Depth meters | Temperature °C. *a* | *b* | Salinity ‰ *a* | *b* | Density $\sigma t$ *a* | *b* | Oxygen cc/L *a* | *b* | Number of specimens[2] |
|---|---|---|---|---|---|---|---|---|---|
| 1,000 | 6.76 | 7.20 | 35.075 | 35.08 | 27.53 | 27.48 | 4.3 | 3.88 | — |
| 1,100 | | 5.92 | | .06 | | .63 | | 4.56 | 1 |
| 1,200 | 5.29 | .30 | 35.08 | .04 | 27.72 | .70 | 5.2 | 5.02 | — |
| 1,300 | | 4.76 | | .03 | | .75 | | .32 | 3 |
| 1,400 | | .52 | | .02 | | .78 | | .60 | — |
| 1,500 | | .18 | | .01 | | .80 | | .80 | 9 |
| 1,600 | 3.96 | 4.00 | 34.99 | 35.00 | 27.81 | .81 | 6.0 | 5.85 | — |
| 1,700 | | 3.90 | | .00 | | .82 | | .92 | 1 |
| 1,800 | | .80 | | 34.996 | | .827 | | .96 | — |
| 1,900 | | .74 | | .993 | | .833 | | .97 | 4 |
| 2,000 | 3.54 | .66 | 35.04 | 34.99 | 27.89 | .838 | 5.9 | .98 | — |

[1] Column *a* gives actual values, taken on Aug. 27, 1931, in the exact center of the circular area in which the hauls were made (Beebe, 1933). The depths at which these determinations were made have been approximated to the nearest 100 meters, from which they differ but little; actual depths were 995, 1,194, 1,593, and 1,993 meters. Column *b* gives the average values for the Bermuda area, compiled by Dr. Gordon A. Riley (unpublished data).

[2] The depth at which a specimen was taken has been approximated to the nearest 100 meters.

smallest previously described finlet of this type was in an animal of mantle-length 18 mm. and had a length of 1.1 mm. Evidently there is some variation in the size at which the transformation occurs.

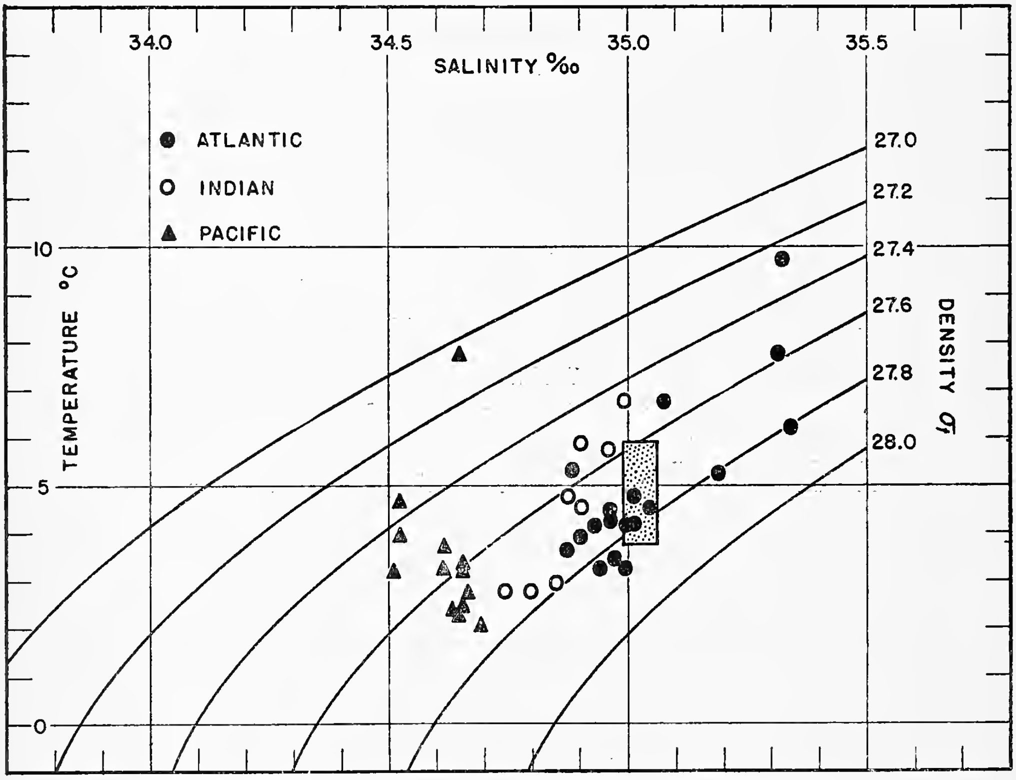
Two of the remaining specimens are in stage 3, the four-finned stage in which the fins are subequal, while the remaining four have passed over into the fourth stage.

It will be noted that in the Bermuda larvae, as in previously described specimens, the average length of the larval fin remains constant throughout stages 2, 3 and 4. The average length is somewhat less than in previously studied specimens, 3.34 as against 3.86 mm. This may be due to the method of preservation as all Dr. Beebe's specimens appear to be somewhat contracted, whereas the *Dana* specimens tended to be relaxed and, possibly, a little swollen from preservation in neutral sea-water formalin. It may also be added that the fin was frequently rubbed and twisted so that measurement was difficult. Apart from this small difference, the thesis that the larval fin virtually ceases to grow after it has been fully formed receives adequate confirmation. The onset of the development of the anterior fin is coincident with the cessation of growth of the larval fin.

The relationship between mantle-length and fin stage is summarized in Table VI. In stage 2, which is represented by an adequate series of specimens, the range and mean mantle-length of the Bermuda series is in remarkably close agreement with the range and mean for those previously described. The agreement is also good for the four stage 4 specimens and the two stage 3 animals are within the range for those hitherto described.

Previous studies of head-width indicates that the head is relatively narrower in larval animals. This receives adequate confirmation from the new material (Table VII). At stage 2 the average head-width index for the Bermuda series is 68.4, as compared with 69.0 for 17 previously described animals. The two stage 3 Bermuda specimens happen to have rather wide heads while the mean for the four stage 4 specimens is below the average for those studied previously. However, in both cases the range is within the known range for these stages and differences in the means must be attributed to the small numbers. All are below the mean values for adults in which head-width is almost equal to mantle-length. The thesis that head-width is relatively narrower in larval animals is fully substantiated.

Great interest attaches to the number of pairs of primary cirri, i.e., the cirri that precede the first sucker, on the arms. The finding for the Bermuda specimens are therefore presented in detail in Table VIII, and ana-




**Text-fig. 8.** The distribution of *Vampyroteuthis infernalis* Chun in relation to temperature, salinity and density. The character of the Bermuda water, from which Dr. Beebe's 18 specimens were taken, is indicated by a stippled rectangle but the individual records are not plotted.

## TABLE V.

### Mantle-length and Other Morphological Characters.

| No. | Mantle-length mm. | Sex | Stage | Head-width index | Ant. fin length mm. | Post. fin length mm. |
|---|---|---|---|---|---|---|
| 78 | 9.5 | ? | 2 | 60.5 | rud. | c.2.1 |
| 79 | 10.0 | ♂ | 2 | 70.0 | rud. | c.3.0* |
| 80 | 10.5 | ♀ | 2 | 81.0 | ? | 3.2 |
| 81 | c.11.5 | ♂ | 2 | 65.2 | 0.4 | 3.0 |
| 82 | 12.0 | ♂ | 2 | 60.8 | △ | 3.5 |
| 83 | 12.5 | ♂ | 2 | 68.0 | 1.0* | c.2.8* |
| 84 | 13.0 | ♀ | 2 | 53.8 | △ | 3.0 |
| 85 | 13.5 | ♀ | 2 | 88.9 | 1.1 | 2.8 |
| 86 | 13.5 | ♂ | 2 | 70.4 | △ | 3.5 |
| 87 | 13.5 | ♀ | 2 | 63.0 | △ | 4.5 |
| 88 | 14.0 | ♀ | 2 | 52.6 | 0.6 | 3.0 |
| 89 | 15.0 | ♂ | 2 | 86.5 | 1.6 | 4.0 |
| 90 | c.15.0 | ♀ | 3 | 80.0 | 4.3 | 3.4 |
| 91 | 18.0 | ♂ | 3 | 94.5 | 8.1 | 5.0 |
| 92 | 21.0 | ♂ | 4 | 76.2 | 6.5 | 3.0 |
| 93 | 22.5 | ♀ | 4 | 77.8 | 6.5 | 4.0* |
| 94 | 23.5 | ♂ | 4 | 78.7 | 10.5 | 3.0 |
| 95 | c.26.0 | ♂ | 4 | 76.8 | Very damaged, ant. prob. 4 times length of post. | |

* Left fin in better condition and measured instead of right.

△ Anterior fin represented by a triangular rudiment, more advanced than the minute bud seen in specimens No. 78 and 79.

## TABLE VI.

### Summary of Data on Mantle-length in Relation to Stage[1]

| Stage | Bermuda collection | | All previous records | |
|---|---|---|---|---|
| | No. | Mantle-length mm. | No. | Mantle-length mm. |
| 1 | — | — | 7 | 5.5-*6.9*-9.0 |
| 2 | 12 | 9.5-*12.4*-15.0 | 18 | 8.0-*12.1*-18.0 |
| 3 | 2 | 15.0-*16.5*-18.0 | 10 | 15.0-*18.1*-26.5 |
| 4 | 4 | 21.0-*23.3*-26.0 | 5 | 19.0-*23.0*-27.0 |
| 5♂♂ | — | — | 15 | 27.0-*40.6*-55.0 |
| 5♀♀ | — | — | 12 | 25.0-*36.0*-63.0 |

[1] Range and *mean* (italics).

## TABLE VII.

### Summary of Data for Head-width Index in Relation to Stage.[1]

| Stage | Bermuda collection | | All previous records | |
|---|---|---|---|---|
| | No. | Head-width index | No. | Head-width index |
| 1 | — | — | 8 | 43.6-*69.1*-95.0 |
| 2 | 12 | 52.6-*68.4*-88.9 | 17 | 51.4-*69.0*-95.0 |
| 3 | 2 | 80.0-*87.3*-94.5 | 11 | 50.0-*69.2*-102.5 |
| 4 | 4 | 76.2-*77.4*-78.7 | 6 | 73.5-*84.5*-97.9 |
| 4-5 | — | — | 6 | 82.5-*98.8*-118.5 |
| 5 | — | — | 21 | 76.0-*93.9*-112.0 |

[1] Range and *mean* (italics).

TABLE VIII.

Number of Pairs of Primary Cirri.

Note: Irregularities are frequent and cannot be described in detail; a cirrus pair is often represented by a single cirrus or, less commonly, by three cirri resulting from bifurcation of one member of the pair.

| | Left arms | | | | Right arms | | | |
|---|---|---|---|---|---|---|---|---|
| No. | 1 | 2 | 3 | 4 | 1 | 2 | 3 | 4 |
| 78 | — | — | Not possible | to count | — | — | — | — |
| 79 | 7 | 7 | 6 | 6 | ?7 | — | 7 | — |
| 80 | 8 | 7 | 7 | 7 | 7 | — | 8 | 8 |
| 81 | 8 | 8 | 7 | 6 | 8 | — | 7 | 7 |
| 82 | 8 | — | 5 | 6 | — | — | 6 | 6 |
| 83 | 8 | 7 | — | 6 | 8 | 7 | 7 | 6 |
| 84 | — | — | — | 8 | 9 | 8 | 9 | 8 |
| 85 | 7 | — | 6 | 6 | 7 | 6 | 6 | 6 |
| 86 | 9 | 8 | 6 | 6 | 9 | 8 | 8 | — |
| 87 | 9 | 7 | 6 | 6 | — | 8 | 6 | 6 |
| 88 | 8 | 8 | 7 | 7 | 7 | 7 | 6 | 6 |
| 89 | 9 | 7 | 7 | 7 | 10 | 8 | 8 | 8 |
| 90 | 10 | 8 | 7 | 6 | — | — | 7 | 7 |
| 91 | 8 | — | — | 6 | 7 | 6 | 6 | 6 |
| 92 | 8 | 7 | 6 | 6 | 8 | 7 | 6 | 6 |
| 93 | 8 | 7 | 7 | 7 | 7 | 7 | 7 | 7 |
| 94 | 7 | 7 | 6 | — | 8 | 7 | 7 | 6 |
| 95 | — | 6 | 6 | 6 | 8 | 6 | 7 | 6 |

lyzed in Tables IX and X. As in previously described specimens, the maximum number of primary cirri is usually on the first arms; a second or third arm may occasionally participate and there is one specimen, No. 80, in which both the third and fourth right arms have as many pairs of primary cirri as the first left, while the first right has one less. This is the first time that a fourth arm has shared in the tabulation of the maximum number of primary cirri.

A further point of interest is that two of the newly described specimens have as many as ten pairs of primary cirri on at least one of the first arms. Among previously described specimens there was evidence that a tenth pair might have been present on the first right arm of the Monaco female (specimen No. 2). In specimen No. 89 of the Bermuda series there can be no doubt that ten pairs occur on the first right arm, the state of preservation being so perfect that there is no possibility of uncertainty. The first left arm has only nine pairs. In specimen No. 90 the first pair on the first left arm is represented by a single cirrus, a frequent abnormality, and this is followed by nine more pairs preceding the first sucker.

In previously described animals the minimum number of primary cirri is shared equally between the third and fourth arms, the first and second arms participating only very occasionally. The same is true of the Bermuda series.

The special interest of the number of primary cirri lies in the fact that Atlantic specimens appear to have an additional pair on all arms. The data for the maximum number will be considered first (Table IX). Many of the previously described Atlantic specimens had a maximum of only seven pairs, but nearly all of the newly described animals have eight or more. The new data therefore not only confirms but amplifies the previous findings. Thirty out of 41 Atlantic specimens have a maximum of eight or more pairs of primary cirri, the peak being at eight, whereas 14 out of the 23 Indo-Pacific specimens have only seven.

The over-all data for the minimum number of primary cirri tells the same story (Table X). Only five out of 26 Indo-Pacific specimens have a minimum of as many as six or more whereas this condition is typical for the Bermuda series, confirming and amplifying the sum total of data for the Atlantic. The analysis of previous material provided some evidence that young Atlantic animals tended to have a smaller minimum number of primary cirri than adults. Nine out of 20 larvae had a minimum of only five pairs whereas none of the seven adults had less than six. Since all the Bermuda specimens are larvae, and all but one have a minimum of six pairs, the hypothesis advanced previously, that there is a difference in this respect between larvae and adults, does not receive confirmation and must be withdrawn.

TABLE IX.

Summary of Data on Maximum Number of Pairs of Primary Cirri.

| | Maximum number of pairs of primary cirri | | | | | Total number |
|---|---|---|---|---|---|---|
| Group | 6 | 7 | 8 | 9 | 10 | specimens |
| Bermuda | — | 2 | 10 | 3 | 2 | 17 |
| Previous Atlantic records | — | 9 | 9 | 6[1] | — | 24 |
| Atlantic *Totals* | — | 11 | 19 | 9[1] | 2 | 41 |
| Indo-Pacific *Totals* | 1 | 14 | 8 | — | — | 23 |

[1] Includes one specimen that may have possessed a tenth pair (Pickford, 1939a).

### Summary.

Eighteen larval specimens of *Vampyroteuthis infernalis* Chun were taken by the Bermuda Oceanographic Expeditions at depths ranging from 1,097 to 1,829 meters. The estimated depth of capture, at one-half the length of the towline, was confirmed with the aid of a bathygraph. No specimens were taken in numerous hauls at depths of less than 1,000 meters, and none were taken in a limited number of hauls at over 2,000 meters The region of maximum abundance, between 1,000 and 1,500 meters (2000 to 3,000 meters towline) is in accordance with previous data for the vertical distribution of this species in the Atlantic, estimated from the length of the towline but without collateral confirmation.

TABLE X.

Summary of Data on Minimum Number of Pairs of Primary Cirri.

| Group | Minimum number of pairs of primary cirri 4 | 5 | 6 | 7 | 8 | Total number specimens |
|---|---|---|---|---|---|---|
| Bermuda | — | 1 | 12 | 3 | 1 | 17 |
| Previous Atlantic records | — | 11 | 16 | 4 | — | **31** |
| Atlantic *Totals* | — | 12 | 28 | 7 | **1** | **48** |
| Indo-Pacific *Totals* | 4 | 17 | 4 | 1 | — | 26 |

Collections were made during the months of April to October; there is a pronounced maximum in June and July, but the interpretation of this is uncertain.

Hydrographic conditions at the known depths of capture are in agreement with the optimum temperature, salinity and density of the water that is characteristically inhabited by this species in the Atlantic. The hypothesis that the species tends to be restricted to a density layer of $\sigma t$ 27.6 to 27.8 is confirmed. The hypothesis that the species is oligoaerobic, as indicated by previous investigations, remains open since Dr. Beebe's specimens were taken in water that was not deficient in oxygen.

The average length of the larval fin is somewhat less than that calculated for previous specimens, 3.34 mm. as compared with 3.86 mm., perhaps due to the state of preservation. The hypothesis that growth of the larval fin virtually ceases at a mantle-length of about 10 mm., concomitant with the appearance of the anterior fin rudiment, is confirmed. The relationship between mantle-length and fin-stage is in agreement with previous descriptions, and the hypothesis that the head-width index is less in larval than in adult animals is confirmed. The hypothesis that Atlantic specimens have one more pair of primary cirri on the arms, as compared with the Indo-Pacific population, is confirmed, but the hypothesis that larval Atlantic specimens have a smaller minimum number of primary cirri than adults must be rejected.

## References.


Beebe, W.

1931a. Bermuda Oceanographic Expeditions 1929-1930. Introduction. *Zoologica,* 13 (1): 1-14.

1931b. Bermuda Oceanographic Expeditions 1929-1930. Individual nets and data. *Zoologica,* 13 (2): 15-36.

1932. Bermuda Oceanographic Expeditions 1931. Individual nets and data. *Zoologica,* 13 (3): 37-45.

1933. Deep-sea fishes of the Bermuda Oceanographic Expeditions. Introduction. *Zoologica,* 16 (1): 5-11.

Coe, W. R.

1945. Plankton of the Bermuda Oceanographic Expeditions. XI. Bathypelagic nemerteans of the Bermuda area and other parts of the North and South Atlantic Oceans, with evidence as to their means of dispersal. *Zoologica,* 30 (3): 145-168.

Pickford, G. E.

1939a. A re-examination of the types of *Melanoteuthis lucens* Joubin. *Bull. Inst. Océanogr. Monaco,* No. 777.

1939b. The Vampyromorpha. A new order of dibranchiate Cephalopoda. *Vestnik Cs. Zool. Spol. Praze,* 6-7: 346-358.

1940. The Vampyromorpha, living-fossil Cephalopoda. *Trans. N. Y. Acad. Sci.,* (2) 2: 169-181.

1946. *Vampyroteuthis infernalis* Chun. An archaic dibranchiate cephalopod. I. Natural history and distribution. *Dana*-Report No. 29.

1949a. *Vampyroteuthis infernalis* Chun. An archaic dibranchiate cephalopod. II. External anatomy. *Dana*-Report No. 32.

1949b. The distribution of the eggs of *Vampyroteuthis infernalis* Chun. *Journ. Marine Res.*: 8 (1): 73-83.

# NEW YORK ZOOLOGICAL SOCIETY

General Office: 30 East Fortieth Street, New York 16, N. Y.
Publication Office: The Zoological Park, New York 60, N. Y.

---

# ZOOLOGICA

SCIENTIFIC CONTRIBUTIONS

*of the*

NEW YORK ZOOLOGICAL SOCIETY

---

VOLUME 35

Part 2

Numbers 6-11

---



Published by the Society

The Zoological Park, New York

August 1, 1950

# CONTENTS

# 6.

# Some Variations in Grouping and Dominance Patterns Among Birds and Mammals.

N. E. Collias.

*University of Wisconsin.*[1]

(Text-figure 1).

The tendency to aggregate is of very general occurrence among animals. Aggressive behavior, in the sense of fighting or threatening and apart from predator-prey relations, is also of quite general occurrence, particularly among the more complex phyla of animals, and for the vertebrates there is sufficient evidence to indicate that aggressiveness is often regulated by means of dominance hierarchies or territorial relations (Collias, 1944; Allee, 1945). The nature of the relationship between the aggregation tendency and the various forms of aggressive behavior does not seem to have been sufficiently investigated and is of special interest since these two general phenomena are often opposed to each other. More information is needed on the relationship of aggressive-submissive dominance relations to grouping patterns.

Another problem concerns the generality and variations of intra- and interspecies dominance orders within given ecological habitats. Considerable data will be required before many generalizations on these topics can be considered secure, and one object of this report is to contribute and to cite additional data for birds and mammals.

These problems ideally should be worked out in the field under natural conditions; however, tentative solutions frequently can be obtained more rapidly from captive animals in large enclosures. Preliminary checking often reveals considerable similarity between the behavior of captive animals and of the same species in the wild. No doubt important differences exist, but at the least, studies on domestic and captive animals could serve as a basis for formulating working hypotheses for related studies in the field. Certainly the converse is also true. More detailed comparison of the results of the present study with field studies will be made later in this article.

The New York Zoological Park maintains a great variety of birds and mammals in large enclosures, and these provided excellent material from which to choose suitable subjects for studies of grouping and dominance patterns.

For the first objective, the study of the relationship between dominance and grouping behavior, two groups of mammals and two of birds were chosen. A group of White-tailed Deer (*Odocoileus virginianus*) was studied as an example of a species which formed small, rather loose groups in which the individuals were often scattered widely over the enclosure. In nature these deer are said to form small groups which may break up at the end of winter; during the rut the buck is usually seen with one doe, occasionally with two or more (Seton, 1929, p. 278). In contrast, a group of Nyala antelopes (*Tragelaphus angasi*) was selected for study because these animals generally formed a compact herd unit. On the African veldt Nyalas live in small troops of one adult male and about half a dozen females. At certain times the females with their young and the immature males herd together, while the adult males wander off singly or in small groups (Fitzsimmons, 1920, p. 122). A small group of penguins gave an example of a species which breeds normally in large, gregarious and compact colonies in which small individual pair territories are marked. A flock of geese of several species gave an example of forms in which wider spacing of breeding pairs is the rule, and also provided opportunity to analyze the organization of a non-breeding and heterospecific flock.

For the second objective, which was to examine in some detail the generality of the dominance principle in a variety of animals from given ecological habitats, observations on the three groups selected were less detailed and systematic. The goose enclosure mentioned above provided an example of a pond habitat, and contained several species of geese, ducks and cranes. A large flying cage contained marsh birds such as herons, ibises and spoonbills as well as many other native and exotic species. A large and grassy

[1] A report submitted to the New York Zoological Society on research done by the author as a Summer Research Fellow of the Society during the summer of 1947 at the New York Zoological Park.

I am indebted to Professor C. R. Carpenter, Research Coordinator of the Society, and to the other Research Fellows for helpful suggestions. My colleagues, Dr. B. F. Riess and Mr. D. Lehrman, generously participated in the full day observations of the geese and penguins. Warm thanks are due Mr. Lee Crandall, General Curator, as well as to other members of the staff and to the various keepers for their helpful advice and ready cooperation. Dr. William Beebe, Director of the Department of Tropical Research, kindly gave me permission to cite some of his unpublished work. Professor Carpenter, Mr. Crandall and Dr. E. B. Hale read the manuscript critically and made many useful suggestions.

enclosure, known as the "African Plains," contained birds and mammals from the African veldt.

### General Procedure.

Grouping relations between the individuals of each species were estimated on the basis of repeated observation. In general these grouping patterns were easily observed and appeared to be quite definite and consistent, and therefore little attempt was made to enumerate instances of contiguity between particular individuals. In a few instances, as in the case of the flock of geese, such impressions of grouping relations were checked by frequent mapping of the relative places occupied by the different individuals when the flock was resting or sleeping.

Dominance relations between individuals were ascertained by enumeration of observed instances of aggressive-submissive interactions, of each individual with all the others. Many but not all of these instances occurred during competition over bits of food provided by the observer or by the caretaker. One animal would attack or threaten another, driving it from the food, and the latter individual was thereupon adjudged subordinate in this particular encounter. In some instances, as in the case of the antelope, aggressive-submissive interactions were observed between males in the proximity of females quite independently of the food supply. In certain other instances of aggressive-submissive interactions, particularly involving penguins, the cause of the interaction was not very evident.

Since for any given pair of individuals in successive encounters the same animal with very few exceptions always dominated the other, it was not difficult to gather sufficient data to establish the great majority if not all of the dominance relations within the group. It was sometimes difficult to ascertain the dominance relations of animals at or near the bottom of the hierarchy since such individuals frequently avoided active competition with the others.

It was more or less obvious to repeated observation that many of the aggressive-submissive encounters of the penguins involved defense of a given area or territory by the owner, and the location of such encounters was added to the tabulation in an attempt to determine the center and limits of the territory. In practice, the territory was determined by noting the area most frequented by a given individual and the degree of its dominance over other individuals on this area. Exceptions to dominance on its usual territory by a given individual were rare, but not infrequently, the presence of other individuals on the more peripheral parts of the territory would be tolerated.

Each group of animals was observed at irregular hours and almost every day. Observation periods for the White-tailed Deer were 15 to 30 minutes long and totalled seven hours from August 4 to September 4. The Nyalas were watched for some 13 hours from August 6 to September 2; as a rule observation periods were 30 minutes long for each day of observation. The penguins were observed for a total of 126 hours between June 21 and September 4. The usual length of the observation period was one hour, but this varied considerably; there was one full day period of observation. The geese were watched from June 23 to September 6, during 61 observation periods, for 38 hours, including one full day. The usual daily observation periods for the geese were either 15 or 30 minutes long. The wading birds in the large flying cage were generally watched for 30 minutes on any one day. Altogether there were 12 such observation periods, making a total of six hours from August 11 to September 3. The birds and mammals of the African Plains were watched simultaneously with the Nyalas whenever they happened to come to the vicinity of these antelopes. Otherwise they were observed more casually and at irregular times.

### White-tailed Deer.

*Description of the White-tailed Deer Group.* This group consisted of two adult eight-point bucks, one spike buck and six adult females. Four fawns were dropped about a month before observations began.

Identification of individuals was relatively easy in the case of the three males because of the form of the antlers. They are here denominated Buck One ($B_1$), Buck Two ($B_2$) and Spike (Sp). In the case of the does, reliance for identification was placed chiefly upon minor differences in coloration or markings. One was named Scar (Sc), the others are denominated White Nose (Wn), Black Nose (Bn), Pale (gray) Nose (Pn), Dark (gray) Nose-Dark Chin (Dnd) and Dark Nose-Light Chin (Dnl).

The history of the group was known to some extent. All deer were removed from the paddock in the spring of 1943, leaving three hand-reared does which could not be caught. About this same time Buck One was received as a fawn and he and the original does are the parents of the other deer with the exception of one tame female given to the Zoo in 1946. This last female tended to keep somewhat apart from the others. Two does were born in the spring of 1945, as was Buck Two. Buck Two was a two-year-old and the spike buck was a little over one year of age when the study began. Unfortunately, in the case of the females, it was not possible to identify the age records for each individual.

The enclosure was roughly rectangular in shape, some 400 feet long by approximately 300 feet wide, giving the deer a range of about three acres. It contained many large deciduous trees but virtually no undergrowth or low ground cover except for a couple of large trees that had been felled near the center of the enclosure. The ground was somewhat rocky and quite uneven, almost

hilly in places. Along one side of the enclosure there flowed a small artificial stream. In addition to the White-tailed Deer, a bull Moose and two cow Moose occupied the enclosure.

*Grouping Relations.* As a rule the White-tailed Deer were scattered widely over the enclosure, either singly or in groups of twos or threes, occasionally of more individuals. There was no observable consistent association of any pairs during the summer. The deer were more likely to congregate somewhat while being fed or while resting, but even then some of the individuals were likely to be in other parts of the paddock.

*Dominance Relations.* Nothing like defense of local areas (territorialism) within the enclosure was seen, but the deer were observed to be ranked according to a definite dominance hierarchy (Table I). Morsels of bread or small pieces of carrot were thrown in among the deer and when they were hungry one would drive the others from the particular bit of food. A doe would abruptly raise one foreleg, bending it at the knee and kicking it forward at a subordinate; if the latter proved recalcitrant, as was occasionally the case, she might then rear up on her hind legs and strike out with both forefeet. However, no fights were seen. The bucks occasionally used the same method but usually they threatened subordinates by dropping the head and lunging at them with the antlers. Rarely a doe was heard to make a low harsh noise or bleat while threatening a subordinate. When threatened, subordinates would retreat and either return, keeping at a safe distance, or else apparently lose interest in the food and move to some other part of the enclosure. Such aggressive-submissive interactions between given pairs of individuals were recorded and summarized and the results are given in Table I and show the dominance hierarchy. The deer are listed in the left hand column of Table I according to position in the dominance hierarchy with the most dominant individual at the top and the least dominant at the bottom.

TABLE I.

Dominance hierarchy of the White-tailed Deer. Aggressive-submissive interactions between dominants and subordinates.

| Dominants | Subordinates | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | $B_1$ | Wn | Bn | Sc | Dnd | Pn | Dnl | $B_2$ | Sp |
| $B_1$ | — | 4 | 31 | 24 | 15 | 24 | 5 | 27 | 14 |
| Wn | — | — | 30 | 18 | 20 | 21 | 2 | 7 | 9 |
| Bn | — | — | — | 23 | 7 | 16 | 11 | 13 | 18 |
| Sc | — | — | — | — | 11 | 11 | 9 | 19 | 7 |
| Dnd | — | — | — | — | — | 15 | 8 | 4 | 7 |
| Pn | — | — | — | — | 1* | — | 1 | 12 | 11 |
| Dnl | — | — | — | — | — | — | — | 6 | 6 |
| $B_2$ | — | — | — | — | 1† | — | — | — | 4 |
| Sp | — | — | — | — | — | — | — | — | — |

* See text.
† Reversal August 30.

It will be noted that one of the eight-point bucks, $B_1$, dominated all of the females, while the younger eight-point buck, $B_2$, was dominated by all of the females during most of the summer when the antlers of the bucks were in velvet. The spike buck (Sp) was dominated by all of the does.

On August 30, $B_2$ was seen to dominate Dnd. It is possible that this was a permanent reversal because while no more interactions were observed, Dnd was not seen to dominate $B_2$ up to the time that observations ceased on September 4. The dominance relationship between the two does, Dnd and Pn, was somewhat unstable. On August 31 Dnd was seen to strike Pn with one fore foot and at once Pn reared up on her hind legs and gave a long low harsh sound, almost a hiss, meanwhile keeping the nostrils closed tightly; when Pn threatened Dnd in this manner the latter retreated. The next day Pn was again seen to threaten Dnd, rearing up on both hind legs, raising both forefeet and making a low harsh sound and at once Dnd retaliated and Pn retreated and left. These two does were seen to have seven aggressive-submissive interactions on the following day, all of which Dnd dominated while Pn failed to threaten back: Dnd was therefore adjudged to be dominant.

In conclusion, the White-tailed Deer in summer formed loose and variable groups, and this fact was associated with the presence of a definite dominance hierarchy based on frequent aggressive-submissive interactions of all the individuals.[2]

## Nyala Antelopes.

*Description of the Nyala Group.* This group consisted of one adult male, one immature male, four adult females and one immature female about two-thirds grown. Identification of individuals was easy in the case of the mature and immature males because of the characteristic pelage and large horns of adult males and smaller horns of immature males. The females are hornless and resembled each other quite closely but could be readily distinguished by differences in markings. The various animals are here referred to as Scar (Sc), Dark Spots (Ds),

[2]Recently (March 24-25, 1950) through the courtesy and assistance of the Wisconsin Conservation Department I was able to visit the overbrowsed deer yards in the Flag River and Brule River valleys of northwestern Wisconsin during the critical part of winter. Here we observed definite signs of a dominance hierarchy among wild White-tailed Deer gathered about bales of hay put out to help save the deer from starvation. Adult bucks generally dominated all the other deer, whereas does and yearlings with a few exceptions dominated the fawns of the preceding year. Aggressive-submissive interactions were also frequent within each sex and age group. Fritz (1929, Board Game Commissioners, *Bull.* 12, pp. 31-35. Penn.) in overbrowsed deer range in Pennsylvania where the deer were not artificially fed, observed a group of deer that were browsing and noted that the older deer constantly chased away younger deer which as a result had difficulty in procuring much food. In both Wisconsin and Pennsylvania it has been noted that winter mortality is much greater for the fawns than it is for other age groups.

Long Spot (Ls), Adult Female (M) and Young Female (Y).

The history of the group was known only in a general way. The adult male and the oldest female (Ds) were the parents or grandparents of all the others and were brought from Africa in 1939. Young were born each year in the Zoo, usually in late December or January. The three adult females were daughters of the original female and two were about four years old and one about 3½ years old. The immature male was born in December, 1945, and was therefore about 2½ years old. The youngest female was only seven months old, having been born on January 1, 1947, to one of the daughters of Ds. The mother would not feed Y, and Y was thereupon transferred to Ds which was pregnant at the time, and later lost her own young one.

The enclosure or paddock known as the African Plains was roughly in the shape of a broad oval, some 325 feet in greatest length and 150 feet wide, comprising a little more than one acre. It was connected at one end with a corral about 100 feet long which adjoined a shelter house which the animals could enter at night. The paddock, like the corral, was covered with grass; it contained a few trees and a small, shallow pool near the center. A number of birds and other mammals shared the enclosure with the Nyalas.

*Grouping Relations.* In general the Nyalas formed a compact group within the paddock, particularly while resting. Generally they moved as a herd when going from one part of the paddock to another, or when going to the shelter house in the evening. Although they might scatter out somewhat while grazing, each member of the herd was usually less than 50 feet from some other member. The one exception to these grouping relations was the young buck, which was generally kept away from the group of females by the old buck. Occasionally the young buck was permitted to join the herd. The females seemed to associate with each other more closely than did any of them with either of the males during the period of observation.

TABLE II.

Dominance hierarchy of the Nyala Antelopes. Aggressive-submissive interactions between dominants and subordinates.

| Dominants | Subordinates | | | | | | |
|---|---|---|---|---|---|---|---|
| | Adult Buck | Young Buck* | Sc | Ls | Ds | M | Y |
| Adult Buck | — | 35 | 4 | 4 | 2 | 1 | 2 |
| Sc | — | — | — | 6 | 1 | 13 | 1 |
| Ls | — | — | 1 | — | 6 | 2 | 30 |
| Ds | — | — | — | — | — | 1 | — |
| M | — | — | — | 1 | — | — | — |
| Y | — | — | — | — | — | — | — |

* Practically no aggressive-submissive interactions were observed between the young buck and the females.

*Dominance Relations.* The dominance hierarchy of the Nyala herd is illustrated in Table II. The adult male frequently lunged at the young buck with his horns and with head down, particularly when the latter came near him and the females, or when a piece of bread or carrot was thrown between the two bucks. The young buck invariably beat a hasty retreat, but since he generally returned near the group after a while, a good number of such aggressive-submissive interactions were observable. Occasionally the adult buck would gently push the females aside with his horns when they went after a piece of bread or carrot directly in front of him, but he never made the vigorous dash that characterized his actions toward the young buck. Even on the relatively few occasions when the young buck was feeding next to the females, practically no aggressive interactions were observed between the young buck and the females.

The females when very hungry and competing for food would butt a subordinate female away from the food with the hornless head, usually striking the subordinate on the flank. At times the subordinate would butt back; sometimes the two would spar momentarily with their heads before the subordinate receded.

The emphasis of this antelope study was placed on the female Nyalas since casual observations suggested the interesting possibility that they were not organized into a definite dominance hierarchy. The animals were then observed regularly from August 6 through August 12 for 30-minute observation periods which totalled four hours. When pieces of bread or carrots were thrown to them, two females would often put their heads close together and munch simultaneously at opposite ends of the same carrot or bread, but with no sign of aggressiveness. During these eight observation periods only one head butt was seen to occur between adult females.

These rare aggressive female interactions suggested the possibility that a dominance hierarchy might be revealed under adequate stress. Therefore, on August 13 and 14 the female Nyalas were penned in the small corral to one side of the main enclosure, where their foods were limited to grass and a little hay. After two days of limited food deprivation the female Nyalas were fed bread, carrots and some grain on the morning of August 15. The bread and carrots were thrown one piece at a time between various individuals. Within half an hour 24 aggressive-submissive interactions were seen among the adult females. Eight of these interactions were contested, i.e. a brief sparring bout with the heads took place. When one individual submitted the other was adjudged to be dominant, at least in that particular contest. All of the aggressive interactions among the adult females occurred with food as the incentive, and therefore the greatly increased aggressiveness of the fe-

males was related to their increased hunger after two days on restricted rations.

The female Nyalas were retained in the corral until the next day and observed for half an hour during the same time as in the preceding day. Pieces of bread and carrot were thrown to them as before, but only two aggressive-submissive interactions were observed. Indeed, only six such reactions were observed following the day the animals were put back on normal rations, in a total of four hours' observation from August 16 through August 23 (30-minute observation periods).

Table II shows that the adult female Nyala Antelopes demonstrate a dominance hierarchy when made hungry by limiting their food. The definiteness of this hierarchy is indicated by the fact that of a total of 31 interactions only two were reversals of the usual dominance order. However, the dominance order was unstable as indicated by the large proportion of the head butts which evoked some retaliation before one of the contestants would retreat.

In conclusion, the adult female Nyala combined a tendency toward close aggregation with a low degree of aggressiveness, since a dominance order was evident only under the stress of food deprivation.

## Penguin Colony.

*Description of the Group of Penguins.* This group contained 14 penguins: 10 Black-footed (*Spheniscus demersus*), 1 female Humboldt (*Spheniscus humboldti*) and 3 hybrids (*Spheniscus demersus* × *humboldti*).

Individuals were readily identified without the use of artificial markings. One of the two adult hybrids was known as Double-band (Db), the other as Single-band (Sb). An immature hybrid was denominated Light-head (Lh), an immature Black-foot was Dark-head (Dh).

The Penguin Enclosure, semi-circular in shape and approximately 40 feet in greatest width, was surrounded by a low, overhanging fence. The area possessed a rocky substratum; about one-half of it was occupied by a deep pool. Four nest boxes, floored with sand and with the open side facing the water, formed a row at one end. The area just in front of the nest boxes was also mostly covered with sand. No other animals were kept in the enclosure with the penguins.

Much of the history of the penguins was known. The group consisted of three original pairs and their Zoo-bred progeny. These three pairs in turn were the remnants of two groups which came in 1941 from the New York Aquarium, or directly from South Africa. One pair was composed of a Black-foot male (originally thought to be a female and named "Annie") which paired with a female Humboldt; the other two pairs were Black-foots. These three pairs had occupied the same nest boxes for several years. They will be referred to as Pairs 1, 2 and 3, and they occupied Boxes 1, 2 and 3 respectively. Pair 2 was the interspecies pair. The fourth box was not regularly occupied, but a pair of hybrid adults (Pair 4), consisting of Db and Sb, occupied it more often than did any of the other pairs. Occasionally, however, when the box was empty, Pair 5, consisting of two Black-foots, B (for "Baldy") and Tp (for its characteristic black patch on the throat) would move in for a while. The sexes of Pairs 4 and 5, of the unpaired adults and of the immature birds, were all unknown.

The hybrids were of course the offspring of Pair 2 and included Pair 4 and the immature bird, Lh. Pair 1 birds were the parents of Pair 5. Dh was the offspring of Pair 3, and although it was six to eight months of age, it was still closely associated with them and was fed fairly regularly by the female, especially during the first part of the summer. The downy young of Pair One was called Y; this bird did not leave the nest box during the first half of the summer. Finally there was one small adult Black-foot of uncertain parentage which, like Lh, did not consistently associate with any other penguin and was quite often solitary; it was labelled S.

*Grouping Relations.* The dynamics of group formation in the penguins could not be completely worked out without experimental analysis but certain deductions seem justified by observation. Grouping depended (1) on the mechanisms responsible for sex-pair and family integration; (2) on the mechanisms responsible for interpair aggregation; (3) on physiological changes associated with the season, such as the moult; (4) on the daily routine to which the birds were accustomed; and (5) on territorial relations. These categories all overlap to some extent; territorial relations are of sufficient importance from the viewpoint of the present study to justify separate and detailed treatment.

It was noted that only members of a pair brayed when close together. Generally when the two birds of a pair were separated and one commenced to bray, the other would proceed directly to its mate, no matter in what part of the enclosure it happened to be, and the two would then bray together. Only members of a pair or their progeny ever preened each other—i. e., nibbled each others' head or neck feathers with the tip of the beak. As a rule only members of a pair engaged in mutual courtship. In the case of pairs with a dependent offspring, the feeding of the young one was a major force in family cohesion.

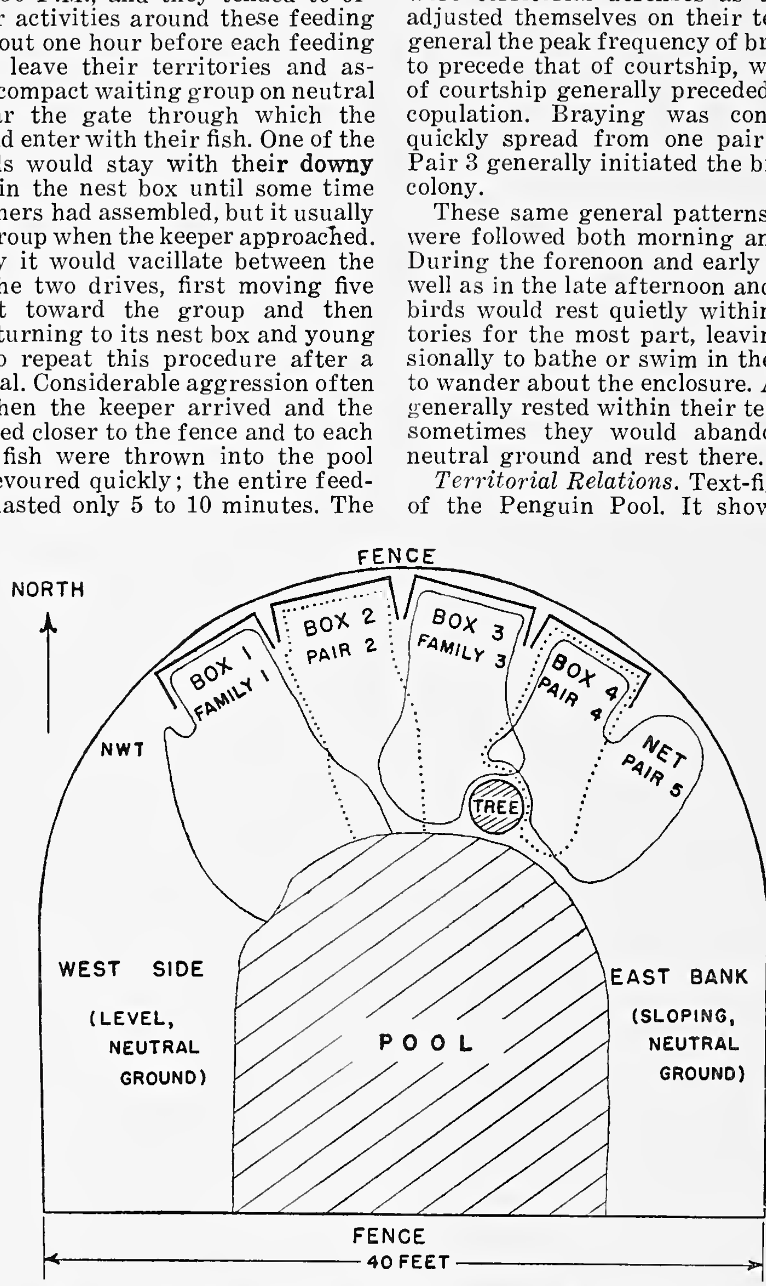
Interpair grouping seemed to be stimulated by hunger, by the coming of nightfall, and possibly by braying. When one pair brayed on its territory the other pairs were likely to go to their own territories to bray. Interpair grouping seemed to be somewhat inhibited or limited by the territorial organization of the colony and by individual variations in the time of bathing or general exploratory behavior. Male 2 ("Annie") was especially independent of the group.

During the late summer the birds moulted, but as a rule only a few individuals at a time would moult. Moulting individuals often stayed apart from the others, away from their mates and territory. A moulting bird would stand quietly and, except at feeding time, seldom entered the water.

The grouping relations of the penguins varied to a considerable degree with their daily routine. Early in the morning most of the birds would bathe. They were generally fed between 9:00 and 9:30 A.M. and again at about 2:30 P.M., and they tended to organize their activities around these feeding periods. About one hour before each feeding they would leave their territories and assemble in a compact waiting group on neutral ground near the gate through which the keeper would enter with their fish. One of the Pair 1 birds would stay with their downy young one in the nest box until some time after the others had assembled, but it usually joined the group when the keeper approached. Occasionally it would vacillate between the effects of the two drives, first moving five or ten feet toward the group and then abruptly returning to its nest box and young one, only to repeat this procedure after a brief interval. Considerable aggression often occurred when the keeper arrived and the birds crowded closer to the fence and to each other. The fish were thrown into the pool and were devoured quickly; the entire feeding period lasted only 5 to 10 minutes. The immature penguins, Y and Dh, usually were fed by their parents just after the adults had fed. Frequently Female One, the mother of the youngest penguin, Y, was the first bird to cease feeding, leave the pool and proceed toward her territory. After the feeding the birds would move into their own special territories and the excitement of the feeding period would merge into a period of braying which generally lasted about an hour. Courtship and a few attempts at copulation were usually observed at this time, as were territorial defenses as the birds readjusted themselves on their territories. In general the peak frequency of braying tended to precede that of courtship, while a period of courtship generally preceded attempts at copulation. Braying was contagious and quickly spread from one pair to another; Pair 3 generally initiated the braying of the colony.

These same general patterns of behavior were followed both morning and afternoon. During the forenoon and early afternoon as well as in the late afternoon and evening the birds would rest quietly within their territories for the most part, leaving only occasionally to bathe or swim in the pool or just to wander about the enclosure. At night they generally rested within their territories, but sometimes they would abandon them for neutral ground and rest there.

*Territorial Relations.* Text-fig. 1 is a map of the Penguin Pool. It shows the boxes




TEXT-FIG. 1. Territories defended by the penguins in the New York Zoological Park colony. NWT refers to Northwest Territory, NET to Northeast Territory. The boundaries of territories 1, 3 and 5 are indicated by continuous lines and those of territories 2 and 4 by dotted lines.

TABLE III.

Location of penguin territorial defenses. **T** = territory; **n** = north half but outside nest box; **s** = south half; e.g. T1n means north half of Territory 1; **Sh** = adjoining shore; **NET** = Northeast territory; **NWT** = Northwest territory. Vocal defenses are not included.

| | In own box | T1n | T1s | T2n | T2s | T3n | T3s | T4n | T4s | NET | NWT | Sh1 | Sh2 | Sh3 | Sh4 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ♂1 | 8 | 46 | 26 | — | 12 | — | — | — | — | — | 1 | 7 | 1 | — | — |
| ♀1 | 6 | 14 | 15 | — | 2 | — | — | — | — | — | — | — | — | — | — |
| Y | 1 | — | 2 | — | — | — | — | — | — | — | — | — | — | — | — |
| ♂2 | 6 | — | 2 | 18 | 6 | 1 | 3 | — | — | — | — | — | 2 | — | — |
| ♀2 | 0 | — | — | 1 | 3 | — | — | — | — | — | — | — | — | 1 | — |
| ♂3 | 1 | — | — | 3 | 3 | 10 | 11 | 1 | 2 | — | — | — | — | — | — |
| ♀3 | 2 | — | 1 | 4 | 11 | 14 | 14 | — | — | — | — | — | — | — | — |
| Dh | — | — | — | — | — | 1 | 2 | 1 | — | — | — | — | — | — | — |
| Sb | 2 | — | — | — | — | — | 2 | 1 | 2 | 1 | — | — | — | — | — |
| Db | 1 | — | — | — | — | — | 2 | 5 | 4 | — | — | — | — | — | — |
| B | 1 | — | — | — | — | — | 3 | 2 | 3 | 9 | — | — | — | — | — |
| Tp | 1 | — | — | — | — | — | 2 | 1 | 2 | 11 | — | — | — | — | — |

occupied by particular pairs or families and the territories which they often kept clear of other penguins. Table III gives the data on which this map is based.

Territories were defended by threatening movements, by vocalizations or occasionally by active attacks. Sometimes the defending bird seized and held the retreating interloper with its beak, while beating it with its flippers; the trespasser as a rule would manage quickly to escape. During the summer fights were very rare but when they occurred the birds would fence very rapidly with their beaks and beat each other with their flippers. Early in the summer Male Two lost one fight to Male One on the latter's territory, and won one fight with Male Three, but the exact site of the latter fight was not recorded. B won one fight over S on the neutral ground of the west side of the enclosure.

When one bird threatened another it would stretch its neck toward the intruder or advance rapidly and directly toward it and the latter would generally retreat at once, frequently going to its own territory. If the two territories adjoined the birds would sometimes bray or yell at each other. Sometimes the threatened bird, after retreating a step or two, would stop, tilt and twist its head so that the face and beak were horizontal, holding this pose for a few seconds. This attitude exhibited a conspicuous pink spot above the eye. Although the function of this pose was not clear it possibly serves to inhibit attack, since no observations were made of a bird being attacked while it maintained itself in this apparently very vulnerable position.

Cooperative attacks in non-vocal defense of the territory by the members of a pair were not common, and were observed only 17 times as compared with 329 defenses by one or the other individual of a pair operating alone (Table IV). However, a definitely larger proportion of merely vocal defenses of the territory were cooperative, and the voice of one partner generally stimulated the other partner to bray, if it was in the vicinity. Because members of a pair often moved about more or less together, they sometimes trespassed and were driven off as a pair; 47 such occurrences were recorded (Table IV).

There were variations in the pattern of individual territories as depicted in Text-fig. 1. In general the territories centered about the nesting boxes, although comparatively few defense reactions within the nest box of a pair were recorded, compared with defenses of the north or adjacent half of the ground between the nest box entrance and the pool. In other words the birds were seen to defend their front yards much more often than they were seen to defend the interior of their houses from intrusion. One possible explanation for this is that whereas territorial boundaries outside the nest boxes were often violated during the ordinary daily movements of the birds, intruders seldom dared to enter a nest box with one or both of the owners in the box or nearby.

Pairs 1, 2 and 3 were older, more dominant and better established than any of the other pairs. In addition, Pairs 1 and 3 each had a young one. These three pairs defended their territories more often (Table III) and spent more time on their territories than did Pairs 4 and 5. These latter two pairs wandered about the enclosure a good deal and as a consequence were often attacked. Pair 4 moved more often as a pair than did Pair 5 and so were more often attacked as a pair (Table IV). Pairs 4 and 5 show considerable territorial overlapping, because both pairs

TABLE IV.

Individual penguins involved in territorial defenses. Trespassers in top row; defenders in column to left. Number of defenses is tabulated. Vocal defenses are not included.

| | ♂1 | ♀1 | Y | ♂2 | ♀2 | ♂3 | ♀3 | Dh | Sb | Db | B | Tp | Lh | S | $P_1$ | $P_2$ | $P_3$ | $P_4$ | $P_5$ | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ♂1 | — | 8 | 1 | 16 | 6 | 11 | 2 | 4 | 2 | 3 | 8 | 2 | 16 | 14 | — | 1 | 7 | 16 | 1 | 117 |
| ♀1 | — | — | — | 9 | — | 14 | 3 | 1 | — | — | 4 | 3 | 2 | 5 | — | — | 2 | 1 | — | 44 |
| $P_1$ | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 0 |
| Y | 17 | — | — | 1 | — | 1 | — | — | — | — | — | — | — | 3 | — | — | — | — | — | 22 |
| ♂2 | 1 | — | 1 | — | — | 2 | 3 | 1 | 1 | 2 | 4 | 2 | 7 | 9 | — | — | 1 | 6 | 1 | 41 |
| ♀2 | — | — | 1 | — | — | — | 3 | — | — | — | — | — | 1 | 3 | — | — | — | — | — | 8 |
| $P_2$ | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 2 | — | — | 2 |
| ♂3 | — | — | 2 | — | 3 | — | — | — | — | 2 | — | 6 | 4 | 9 | — | — | — | 2 | 2 | 30 |
| ♀3 | 2 | 1 | — | 2 | — | 1 | — | — | — | — | 7 | 6 | — | 37 | — | — | — | — | 1 | 57 |
| P3 | — | — | — | — | — | — | — | — | — | — | — | — | 3 | 1 | — | — | — | — | — | 4 |
| Dh | 1 | — | — | — | — | — | — | — | — | — | 1 | 1 | 1 | 3 | — | — | — | — | — | 7 |
| Sb | — | — | — | — | — | — | — | — | — | — | 1 | — | 2 | 2 | — | — | — | — | 1 | 6 |
| Db | — | — | — | — | — | — | — | — | — | — | 3 | 1 | — | 1 | — | — | — | — | 1 | 6 |
| P4 | — | — | — | — | — | — | — | — | — | — | — | — | 1 | — | — | — | — | — | 1 | 2 |
| B | — | — | — | — | — | — | — | — | — | 2 | — | — | 3 | 1 | — | — | — | — | — | 6 |
| Tp | — | 1 | — | — | 2 | — | — | — | — | — | — | — | — | 4 | — | — | — | — | — | 7 |
| P5 | — | — | — | 1 | — | 1 | — | — | 1 | — | — | — | 5 | — | — | — | — | 1 | — | 9 |
| Total | 21 | 2 | 4 | 28 | 11 | 29 | 11 | 6 | 4 | 9 | 28 | 21 | 50 | 92 | 0 | 1 | 12 | 26 | 8 | |

would defend Box 4 and the ground in front of it. This may well be related to the fact that during the preceding year B of Pair 5 was mated to one of the Pair 4 birds and occupied Box 4 with this bird. Pair 4 dominated Pair 5 and was able to evict Pair 5 from Box 4 and from the area just in front of the box. Perhaps as a result of this Pair 5 centered their defenses in the area called the Northeast territory which adjoined Box 4 and Territory 4. The two unmated adults, S and Lh, did not have any regular territory and very rarely did they bray, their rare vocalizations consisting merely of low moans.

In general territorial overlap was greatest in those parts of the territories near the shore of the pool away from the immediate vicinity of the nest boxes. There were several reasons for this: these areas were the usual resting places for most of the pairs, and they also formed a highway for overland movement to and from the neutral ground, particularly the West Side. Such movements facilitated contacts and most of the territorial defenses were seen in the period of readjustment following the general feeding periods in the morning and afternoon. The birds would defend the vicinity of their usual resting places and this made it appear as if they sometimes defended the adjoining parts of their neighbors' territories, particularly when the neighbors were absent from these areas. Pair 2 spent much of its time in Box 2 and Pairs 1 and 3, which often rested in the south part of their own territories, tended to spread their territories over the southern part of Territory 2. Another complicating factor was the frequent presence on the south part of Territory 2 of S, a solitary, unmated and relatively young adult. The members of Pairs 1 and 3 dominated S, and as a result of the attempt of S to settle between them they often threatened and drove S. Any considerable overlap between Territories 3 and 4 was somewhat nullified by the presence of a large tree between the south parts of these two territories.

In contrast, territorial boundaries in a few places were very sharp, particularly between the north part of Territory 1 and 2. Male 2 was continually encroaching at this boundary and was as persistently driven back by one or the other of the Pair 1 birds. As a rule Pair 1 kept strictly out of the north half of Territory 2.

The two unmated birds, S and Lh, wandered about more than did any of the other birds, and were more often driven from the territories than were any of the mated birds (Table IV). Lh spent a relatively high proportion of its time in the pool, as compared with the other birds.

The males defended a more extensive area than did their female mates (Table IV) and in the case of Pairs 1 and 2 the males defended the territory much more frequently than did the female (Table IV). However, in the case of Pair 3 the female defended the territory much more than did the male. About one-half of the 112 observed territorial defenses by Male 1 were against other males showing interest in Female 1 or else against S and Lh which attempted to establish standing places near the south half of Territory 1. S tried to locate a little closer to Territory 3, and the great majority of the territorial defenses of Female 3 were against S. Most of the territorial defenses of Female

1 were against males apparently attempting to "flirt" with her, i.e., Males 2 and 3. These males seemed also to be attracted by the squeaking or "food-begging" vocalization of the young penguin in Box 1, and they would not infrequently move toward Territory 1 when Y was calling for food.

Of special interest are 17 threats or pecks directed by Y against his parent, Male 1. It is quite possible that these pecks are of actual territorial significance, since they occurred on Territory 1. Male 1 was in moult at the time and his appearance had changed considerably, while 60 mgm. of male hormone (testosterone propionate)[3] had been implanted in Y. In contrast, Y directed none of his attacks against Female 1 which was not in moult. Female 1 was generally near Y so it is also possible that his attacks on his father were related to sex jealousy. Interestingly, Male 1 tolerated these attacks from his progeny.

Dh, the young penguin of Family 3, pecked at his mother 32 times and at his father 15 times on Territory 3, but these pecks were all associated with active food-begging by Dh and it seemed almost as if Dh were trying to attract the attention of his apparently indifferent parents. However, the aggressive behavior of Dh towards its parents could be interpreted in other ways, e.g. as food frustration, since Dh had apparently not yet learned to feed itself.

The penguin territories on the whole had been established for a long time. Territories 1, 2 and 3 at least were very stable and apparently did not often need to be defended by active threat or attack. On June 27, Family 1 was watched all day (16½ hours) and during this time Male 1 defended the territory only 6 times, Female 1 defended the territory only 8 times. All defenses occurred before 2 P.M. However, Male 1 on another day was once seen to chase a bird off his territory at 10:15 P.M., well after nightfall.

A certain degree of either general excitement or of specific drive is perhaps necessary for territorial defense. Very early one morning Male 1 was seen to permit Pair 4 to enter his box while he was inside lying on the nest. Pair 4 left but soon returned, and then repeated this behavior. Male 1 merely looked at them each time, but after the 4th intrusion he abruptly arose, seized one of the Pair 4 birds with his beak and beat it vigorously with his flippers. In fact all of the behavior patterns of the penguins were likely to be more or less fragmentary and incomplete at times apparently depending on the level of excitability reached by the birds as well as on other factors. Braying seemed to excite the birds, and one of the most effective of all stimulus situations causing territorial defense was the braying of trespassers on the territory. For example, one day Family 3 brayed on the south part of Territory 2 not far from their usual resting place on Territory 3; at once Male 1 ran out of Box 1 into Territory 2 and threatened them. They stopped braying but stayed where they were and he returned to Box 1. When trespassers brayed while actually on Territory 1 Male 1 as a rule actively attacked them.

Certain incidents threw some light on the value of territory to penguins. For one thing it helps protect the nest. One afternoon while all the other penguins were in another part of the enclosure Male 1 was seen to enter first one undefended nest box and then another, each time removing some nest material (largely twigs) to his own box. He worked continuously and in 15 or 20 minutes had removed practically all of the nesting material in the colony to his own box. Another value of territorial establishment and maintenance was seen during the rare occasions when both parents of Family 1 left their young one all alone in Box 1. Male 2, and once Pair 2, thereupon entered Box 1 and bit the young one. Thus, territorialism relates to protection and survival of the young.

*Dominance Order.* Roberts (1940) observed some signs of possible dominance order in Gentoo Penguins in nature. At the New York Zoological Park it was found that the penguins had a definite dominance order while on neutral ground. The data are given in Table V, which tabulates the frequency with which any given penguin was seen to peck or threaten on neutral ground various other individuals which in turn retreated. The scarcity of such aggressive-submissive interactions is noteworthy; only 391 such interactions were recorded during some 126 hours of observation, an average of little more than 3 per hour. One reason for this was that the birds spent much of their time within their own territories. Another is the fact that food competition in the penguins seemed to have very little dependence on aggressive behavior, unlike the case in most other species of birds in which dominance hierarchies have been studied. The bird that could secure the greatest number of fish in the pool in the shortest time got the most, and the bucket of smelts as a rule disappeared within 5 or 10 minutes once it was emptied into the water. Fish placed on the ground were frequently ignored. It was, however, true that a relatively large proportion of the pecking and threatening took place in the highly excited group just before feeding. Reverse pecks or threats of a normally subordinate bird against a dominant bird were rare; such reactions were most likely to occur in the excited and crowded group just prior to feeding.

From Table V it is apparent that the three oldest males held the three highest ranks in the dominance order, while the youngest birds tended to be at or near the bottom. The three oldest females ranked fairly high. In a few cases dominance relations were not worked out, and in one case, that of Lh versus S, (both unmated birds), the dominance relations were apparently unstable.

---

[3] I am indebted to the generosity of the Schering Corporation, Bloomfield, N. J., for this hormone.

TABLE V.

Dominance order of penguins on neutral ground. Dominators in left-hand column, birds dominated in row above; frequency of aggressive-submissive reactions (pecks or threats plus retreat of other bird) are tabulated.

| | ♂1 | ♂2 | ♂3 | Sb | ♀1 | ♀2 | Db | ♀3 | Lh | B | Tp | Dh | S | Y | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ♂1 | — | 3 | 8 | 11 | 3 | 5 | 10 | 6 | 14 | 7 | 3 | 3 | 5 | 1 | 89 |
| ♂2 | — | — | 2 | 3 | 1 | — | 3 | 2 | 2 | 1 | 2 | — | 3 | 2 | 21 |
| ♂3 | — | — | — | 3 | 1 | 1 | 3 | 1 | 5 | 7 | 2 | — | 3 | 2 | 27 |
| Sb | — | — | — | — | 6 | — | 4 | 4 | 34 | 11 | 3 | 1 | 6 | 2 | 71 |
| ♀1 | — | — | — | 1 | — | 3 | — | 3 | 4 | 5 | — | 1 | 3 | — | 20 |
| ♀2 | — | — | 1 | — | — | — | 1 | 1 | 8 | 6 | 1 | 1 | 7 | 1 | 27 |
| Db | — | — | — | — | — | — | — | 1 | 7 | 7 | 3 | 1 | 1 | 2 | 22 |
| ♀3 | — | — | — | — | — | — | — | — | 6 | 3 | 2 | — | 3 | — | 14 |
| Lh | — | — | — | — | 2 | — | 4 | — | — | 17 | 9 | 2 | 8 | 4 | 49 |
| B | — | — | — | — | — | — | — | — | 2 | — | — | — | 10 | 1 | 14 |
| Tp | — | — | — | — | — | — | — | — | 3 | — | — | — | 7 | 2 | 12 |
| Dh | — | — | — | — | — | — | — | — | — | — | 1 | — | 6 | 1 | 8 |
| S | — | — | — | — | — | — | — | — | 11 | — | — | — | — | 2 | 13 |
| Y | 2 | — | — | — | 2 | — | — | — | — | — | — | — | — | — | 4 |
| | | | | | | | | | | | | | | | 391 |

The relations of the dominance order on neutral ground to fixed or established territories are of special interest (Tables IV and V). The three oldest males not only were at the top of the peck order but they also held, with their mates, the most stable and most frequently defended territories. The top bird in the dominance order, Male 1, defended the largest territory. The younger and unmated birds not only were at or near the bottom of the dominance order, but in addition they did not hold territory, although Lh and S tended to rest persistently in certain places. Pairs 4 and 5, which held unstable territories which they occupied and defended rather infrequently, were intermediate in the dominance order.

The territory-holding penguins defended their territories against birds higher in the dominance order 40 times in contast to 284 defenses against birds lower in the dominance order. If we omit the 117 territorial defenses of Male 1 which was the top bird in the dominance order and which had no dominator, the number of territorial defenses against subordinates is reduced to 167, which is still more than four times the number of defenses against dominators. One reason why the penguins did not often defend their territories against birds above them in the dominance order is probably related to the relatively infrequent trespassing by the more dominant birds on the territories of the lower-ranking birds. The enclosure was so arranged that in coming and going by way of land to the usual resting and waiting place on the West Side, most of the penguins had to pass through territories of the dominant males rather than through the territories of the relatively subordinate Pairs 4 and 5. However, the East Bank, also neutral ground, was frequently visited and quite often the birds would return overland to their territories, so this explanation is probably not sufficient to explain completely why territories were defended relatively infrequently against birds of higher rank in the dominance order. Male 3 was actually seen to retreat from threats of Male 2 on the territory of Male 3 on two occasions.

Occasionally the birds were seen to defend standing or resting places on what was normally neutral ground. One morning a small boy climbed into the enclosure to get his ball and in doing so he frightened the penguins over to the East Bank where they stayed in a group for well over an hour. Soon it was noticed that the birds were starting to defend the places on which they had settled, particularly when a bird attempted to change places. Subordinate birds even brayed at or threatened birds above them in the dominance order whenever the dominants moved near them. For example, Pair 5 brayed at Pair 1 which brayed back briefly; and when Male 3 moved near Pair 4, Sb brayed at him, Male 3 brayed back, and these two birds then exchanged threats and pecks, and again brayed at each other.

Many of the aggressions on neutral ground were by males. However, the males rarely or never pecked or threatened their mates although they spent far more time in close association with their mates than with any other birds. Occasionally the members of a pair were seen to clatter their beaks together while facing each other; it looked as if the birds were fencing rapidly with their

beaks. The interpretation of this behavior is not clear, although it has been considered as courtship behavior (Kearton, 1930). However, the type of courtship behavior that is most frequent and which was seen to be followed by mounting and copulation, is different. Usually courtship is apparently initiated by the female which parades in an arc before the male with neck arched and beak lowered; the male follows and places his throat and beak closely over the head of the female and works his way behind her while gently slapping her front and back with his flippers, meanwhile vibrating his head and beak over the top of her head. When he gets around behind the female he keeps placing one foot on her back as if "urging" her to lie down; if she does so he will mount. This pattern may be prevented or brought to an abrupt end by the bill clatter which, it seemed, was often initiated by the female's raising her beak upward and so preventing the male from holding his head in the normal courtship position. The resemblance of the bill clatter to the fighting pattern of the birds suggests the possibility that instead of being courtship behavior it could well be interpreted as a form of aggressive behavior, possibly related to sex frustration.

It is possible that the normal greeting ceremony between male and female of a pair serves to inhibit attack. Roberts (1940) observed that a stuffed Gentoo Penguin placed on a nest with eggs or chicks almost invariably elicited the normal greeting bow and hiss of this species from whichever of the two owners returned first. The intruder was then attacked, presumably because it was unable to respond with similar behavior. On a few occasions Male 1 was seen to peck and drive his own mate, Female 1, out of Box 1 shortly after she had entered, and on one of these occasions it was noted that the bowing ceremony of the female was omitted; on the other occasion the female bowed twice, as did the male, but she held her head and beak verv high afterward. Bowing seemed to bear some relation to the nest site since it was frequently omitted when the birds of a pair came together away from the nest after a period of separation. Mutual braying, however, was rarely omitted. Occasionally when mates came together the male proceeded at once to court the female, omitting both bowing and braying ceremonies.

One incident occurred which indicated that the male may occasionally defend his female mate. Male 2 often encroached on Territory 1 and one day while Male 1 was absent he was unusually persistent in approaching Female 1, who was attempting to feed her young. This persistence of Male 2 continually diverted Female 1 from her young one while she drove Male 2 back to his own territory. Male 2 seemed to become bolder and actually entered Box 1 and when Female 1 threatened him, instead of retreating out of Box 1 he pecked at her. Female 1 thereupon uttered a low moan and immediately her mate, Male 1, left the assembly of penguins on neutral ground some 20 feet away, ran to Box 1 and drove away Male 2.

Although cooperative braying by mates was common in vocal defense of their territories, actual cooperative threats on neutral ground were rare. One day Pair 4 were seen swimming side by side in the pool and braying at and chasing Male 2. One of the Pair 4 birds (not identified) actually pecked Male 2, which ordinarily dominated both members of Pair 4. Male 2 circled about and left the pool at the place where his own territory adjoined the shore.

The question arises as to the basis for high social rank in the penguins. Sex was one such factor, since the males generally dominated females. Age is another highly important factor—the oldest birds held the highest ranks. Large size was a possible factor and was roughly associated with high rank. The birds were not weighed, but the Humboldt female and her hybrid offspring, Pair 4 and Lh and the three top males 1, 2 and 3, which were about the same size, were the largest birds; Females 1 and 3, and Dh were definitely smaller birds, while the smallest of all were Pair 5 and S. While male sex, greater age and larger size were all associated in general with higher rank in the dominance order, to what extent each factor was directly meaningful for high social rank could not be decided.

In summary, the grouping pattern of the penguins depended to a large extent on their system of territorial relations as based on individual sex pairs or families. Important modifying factors were related to the dominance hierarchy, the daily routine of feeding, bathing and general movement about the enclosure, the attraction between birds of different pairs, and physiological seasonal changes such as the moult. The penguins showed no direct aggressive competition for food items, unlike the other animals studied at the New York Zoological Park.

## The Flock of Geese.

*Description of the Group.* This group consited of one Pink-footed Goose, six Barnacle Geese, one pair of Lesser Canada Geese, one pair of Cackling Geese and one pair of Black Brants. Late in the summer one pair of Blue Geese was added.

Identification of individuals within each species without marking them proved to be difficult, although the degree of development of the white collar at the base of the black neck was very helpful in the case of the Lesser Canada and Cackling Geese. At first aniline dyes were used to color some of the lighter portions of the plumage; most of the dye washed off within two or three weeks, and then colored leg bands were used.

The six Barnacle Geese came from a purchase of two in 1927, and a gift of five in 1942. They were kept in another enclosure where they reared four young in 1942 and

1944. In 1945 they were moved to the enclosure in which they were kept at the time of this study and subsequent mortality reduced them to their present numbers.

The Blue Geese were definitely larger than any of the other geese and they were removed from the enclosure in early spring because they had been aggressively driving the other geese about and apparently preventing attempts to breed by the latter. The Blue Geese were returned late in the summer after one pair of Barnacles had laid and made an unsuccessful attempt to rear young. The rest of the geese were present in the enclosure continually and, with the Blue Geese, all had spent the winter together.

The enclosure was roughly oval, about 225 feet long and 100 feet at its greatest width, comprising approximately ½ acre. About one-half of the area was occupied by a pond. The rest contained a good scattering of shrubby and herbaceous vegetation as well as a number of small trees. The enclosure was merely fenced in at the sides and the birds were confined by wing-clipping. In addition to the geese and brant there were three Demoiselle Cranes, a South African Sheldrake and a Yellow-billed Duck in the enclosure, while a varying number of semi-domesticated Mallards and Black Ducks often flew into and out of the enclosure.

*Grouping Relations.* In general all of the geese were likely to come together while resting and sleeping and to a lesser extent while feeding, competitive intolerance in the latter activity preventing as close flocking as during the former. The flock as a whole could readily be recognized as being organized into sub-groups composed of the different species and sex pairs. Thus the Barnacles associated with each other more often and more closely in the non-breeding flock than they did with any of the other species. In turn, the six Barnacle Geese were divided into two pairs, each with one other individual adherent. Br (male) was mated to Bb (female) and Bg attached itself closely to this pair. Bp (male) possibly was paired with By, and Bu tended to be with them more often than with the other group of three Barnacle Geese, perhaps more through exclusion by Br than by preference for Bp and By. Unfortunately, only the sex of Br, Bb and Bp was definitely determined, nor were the former family relations of these geese known. Although the pair of Lesser Canada Geese, Lu and Lg, associated together more often and more closely than did either of them with any of the other geese, they did not form nearly so close a pair as did the two Cackling Geese, Cy and Cr. The two brants, Rbt and Bbt, like the two Lesser Canada Geese, were likewise a relatively loose pair.

It was found that one of the best ways to study the grouping relations of the geese was to map the distance between different individuals when they sat down to rest, as they usually did during the forenoon. Another method was to note which individuals joined and left the main flock of feeding or resting geese in constant pairs or subgroups. Frequently certain individual geese wandered about the enclosure together but apart from the other geese. All of these clues, repeatedly observed, made it possible to decide the preferential grouping patterns of the geese. When this was done for all the geese there resulted the interesting hypothesis *that the degree of association tended to parallel the degree of similarity in appearance of the species.*

Lesser Canada and Cackling Geese, which very closely resemble each other and are considered races of the same species (A.O.U. Checklist of North American Birds, 1931), were more often together than with other species. In turn these geese associated more closely with the Barnacle Geese than they did with the Black Brants which have rather short necks for geese and lack white markings on the head; white head markings, although more extensive in the Barnacle Geese, were also present in Lesser Canada and Cackling Geese. The Pink-footed Goose, which resembled the others least of all, was most often apart from the main flock of the other geese.

It is possible that this general association pattern connects with the history of contiguity of these particular individuals rather than having any significance with respect to species recognition cues. However, a similar phenomenon was noted for five different species of pelicans which were confined to a 1½ acre pond at the Zoo; in this group the more similar species roosted together each night. Thus the American and European White Pelicans, both predominantly white species, roosted together with the pale gray Dalmatian Pelican (from southeastern Europe and Asia) on the same rocky islet in the pond. The Eastern Black-backed Pelicans (Australia), which have black and white plumage, roosted together in another part of the pond, while several California Brown Pelicans roosted in various other places still more remote from the first group. These roosting spots were observed for some 20 different evenings and remained quite consistent.

The geese showed a strong tendency to engage in any given form of behavior as a group. For example, they would often feed more or less together, preen themselves at the same time, lie down and rest together and move about the enclosure together, either on land or in the pond. Occasionally they would splash about in a circle in the pond and these rather uncommon periods of increased activity soon tended to involve the entire group. It was as if almost any form of behavior was contagious and tended to induce the same type of behavior in all other geese.

Br, a male Barnacle Goose, was consistently followed by his mate, Bb, and by their hanger-on, Bg, as he moved about the enclosure. Sometimes the rest of the geese,

particularly the rest of the Barnacles, would follow this group of three. However, no very consistent and obvious leadership was present for the flock of geese as a whole. Indeed, as mentioned above, this flock often broke up into subgroups, composed mainly of sex-pairs.

*Influence of Breeding Activities on Grouping Behavior.* One breeding pair of Barnacle Geese, Br and Bb, left the flock and became strongly territorial from the start of their nesting about June 25 in one end of the enclosure until their clutch of six eggs hatched on July 25. Only one gosling survived this day, and the rest of the eggs or goslings disappeared. Bb did all of the incubating while Br stood guard, usually a few feet before the water entrance to the nest which was located a few feet from the margin of the pond. He permitted no other geese or ducks to come near Bb and her nest, with the exception of Bg.

On July 10 this pair of geese was kept under continuous observation all day from 4:50 A.M. to 10:00 P.M., a total of some 17 hours. During this day Br deserted his post for only 36 minutes, involving some 20 brief excursions out of his territory to the general feeding spot of the geese. His longest continuous period of absence was less than six minutes. He defended his territory 79 times, including 19 defenses against encroachment by Black Ducks and Mallards. Most of the difficulty encountered by Br with the other geese seemed to come from the interference with their daily routine which was caused by the inconvenient location of the nesting site. During the early morning the geese would frequently swim about in the pool not far from the neighborhood of the nest and in the late evening they tended to congregate in the same place where they had been accustomed to spend the night; whereas during the remainder of the day they were usually to be found browsing about or resting on land. This routine is reflected by the occurrence of 65 out of the total 79 territorial defenses by Br in the periods from 5 to 9 A.M. or from 7 to 10 P.M. Almost every time that Br drove the other geese out of "his" end of the pool they would soon return, as a rule with By leading the way. In driving off the other geese, Br would threaten them with open mouth and would honk loudly.

Br showed a remarkable tolerance for Bg, against which he gave only one honking defense during the entire day and which he permitted to remain in his immediate vicinity. Frequently he was seen to pass close by Bg in order to drive away the other geese, without molesting Bg. The basis of this tolerance association was not clearly understood. It was noted in the first few days of the nesting that Bg persistently accompanied Br and Bb about the enclosure and although Bg was often driven off at that time she offered only passive resistance, moving off and soon returning.

With the coming of nightfall Br's social drives apparently began to overcome those related to possession and defense of territory, and he gradually swam about 30 feet to join the flock outside of his territory. He then drifted back slowly with another Barnacle Goose, gradually followed by the rest of the geese, into their usual sleeping place in the end of the pond, which included Br's territory.

During the 17 hours of observation on July 10, Bb left her nest three times for a total of only 30 minutes—from 7:46-7:50 A.M. to drink; 11:55 A.M.-12:08 P.M. and 5:15-5:28 P.M. to feed. She took almost no part in the defense of the pair's territory, although she would honk loudly when Bg came close to the nest. In general she seemed

TABLE VI.

Dominance order of the flock of geese. Dominant birds are listed in column to left, birds threatened are in top row; numbers of threats are tabulated. Assumed pairs are grouped close together in left hand column.

| | Pf | Br | Bb | Lu | Lg | Cy | Cr | Bp | By | Bu | Bg | Rbt | Bbt | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Pf | — | 43 | 36 | — | 5 | 32 | 11 | 3 | 3 | 12 | 11 | 2 | 0 | 158 |
| Br | — | — | 1 | 6 | 13 | 30 | 11 | 9 | 5 | 23 | 23 | 5 | 4 | 130 |
| Bb | — | — | — | 0 | 1 | 1 | 1 | 0 | 1 | 5 | 25 | 0 | 2 | 36 |
| Lu | 21 | — | — | — | 13 | 28 | 22 | 8 | 10 | 18 | 11 | 8 | 3 | 142 |
| Lg | — | — | — | — | — | 38 | 14 | 7 | 5 | 13 | 11 | 6 | 5 | 99 |
| Cy | — | — | 1 | — | — | — | 4 | 1 | 17 | 36 | 11 | 17 | 10 | 96 |
| Cr | — | — | — | — | — | — | — | 0 | 0 | 2 | 3 | 13 | 5 | 23 |
| Bp | — | — | — | — | — | — | — | — | 1 | 3 | 4 | 0 | 0 | 8 |
| By | — | — | — | — | — | — | — | — | — | 19 | — | 0 | 0 | 19 |
| Bu | – | — | — | — | — | — | — | — | — | — | 17 | 3 | 1 | 21 |
| Bg | — | — | — | — | — | — | — | — | 13 | — | — | 2 | 1 | 16 |
| Rbt | — | — | — | — | — | — | — | — | — | — | — | — | 1 | 1 |
| Bbt | — | — | — | — | — | — | — | — | — | — | — | — | — | 0 |

to be less tolerant of Bg than was Br during the summer's observation (cf. Table VI). Bb spent the night on her nest.

When the gosling hatched Br seemed to lose all interest in the nest site, but instead kept all the other geese away from the vicinity of Bb and her gosling with the same energy which he had previously devoted to the defense of the nest site. The gosling closely followed its mother about. She kept up a low grunting or grumbling sound, which was apparently the equivalent of the clucking of a broody hen, as she browsed about.

That the gosling was the stimulus to Br's excessive aggressiveness toward the other geese was demonstrated by an accidental incident which occurred the day after it hatched. On this day the gosling was found in another part of the Zoo by Headkeeper of Birds George Scott, who returned it to its parents. In the meantime, Br and Bb were observed by Mr. Scott to be flocking with the other geese, but the moment after their gosling was returned to them, Br and Bb at once drove off all the other geese and kept them from the immediate vicinity of the gosling.

The function of this aggressive isolation of the young from the other geese was demonstrated by the tendency of Bg, which was still often permitted to associate with Br and Bb, to peck and bite at the gosling. This was observed several times but the parents merely honked at Bg without attacking. Four days after the gosling hatched, Pf was seen to threaten the family—Br had lost the dominance over Pf which he had maintained with his territory, and from this time on to the end of the summer's observations Pf seemed to show a special antipathy to Br and Bb (Table VI). What their dominance relations to Pf had been before Br and Bb started nesting was not known. Whenever Pf threatened Br and Bb the gosling was likely to be left alone temporarily and when this occurred Bg was occasionally seen to bite the gosling. It seems not unlikely that these events were responsible for the death of the gosling, which occurred when it was six days old. Pf was seen chasing the parents which kept circling about a shrub that stood over the dead gosling. After the dead gosling was removed the parents moved about the enclosure for some time honking loudly at intervals of a few seconds, but later in the day they were seen to have rejoined the flock.

*Dominance Relations in the Flock.* Dominance was expressed by one bird advancing toward another, which it threatened with open beak, with head held low and with neck extended except for its base which was drawn backward slightly. Meanwhile the subordinate bird would retreat; rarely it stood its ground until attacked. The numbers of such reactions observed were tabulated and the results are shown in Table VI for all species of geese in the enclosure. About 11 per cent. of the threats were made on two individuals simultaneously, which were usually a sex pair. Each such threat is tabulated separately for each of the two birds threatened.

It may be noted that dominance-subordination relations within the species and between species of geese were frequent and pronounced. It should also be noted that these dominance relations were consistent for any given pair of individuals and no reversals occurred during the period of observation, except for the territorial case already described.

From June 23 to July 18 a total of 14 hours of observation of the geese at various places in the enclosure, including the spot where they were usually fed, yielded a total of only 45 threats, including intra- and interspecies contacts. Thereafter, to facilitate observation of dominance relations, pieces of bread were tossed between selected geese in the period from July 21 to September 2. This covered a total of 16½ hours (not including the all-day observation on July 10) during which a total of 591 threats were observed between the geese. It is evident that placing the birds in a specific food competitive situation by means of this technique increased the frequency of aggressive interaction more than ten-fold.[4] At the same time this method merely brought out the already existing dominance order, since none of the 45 aggressive-submissive interactions previously observed were at variance with the dominance relations observed during the later observation periods. These 45 encounters involved 24 of the 78 possible paired relations among the 13 geese of Table VI.

Several interesting relationships may be observed by inspection of Table VI. In this table the presumed sex pairs or mates are grouped together; i.e., birds which associated much more closely with each other than with other geese in the enclosure. The scarcity of threat reactions within sex pairs is noteworthy, particularly in the breeding pair of Barnacle Geese, Br and Bb, and in the pair of Cackling Geese, Cy and Cr. It is not evident from the table in the case of the pair of Lesser Canada Geese, Lu and Lg. However, it was not infrequently observed that when the Pink-footed Goose attacked Lg, that Lu would immediately attack Pf, often coming 10 or more feet to do so.

The tolerance of one mate for another is also of interest in view of the fact that only one pair of the geese made any attempt to breed. This pair, Br and Bb, were near the top of the dominance order in the flock as shown in Table VI, which for this pair includes only their *non-territorial* interactions with the other geese. The male, Br, delivered

[4] An interesting parallel to this increase of aggressiveness with increased food competition has been observed under natural conditions, by R. C. Hopkins for Canada Geese on Horicon Marsh, a famous refuge for waterfowl in Wisconsin (1947, *Wis. Wildlife Res. Quart. Rpts.*, 6:14-23. Wis. Conservation Dept.). Numerous instances were noted during goose-trapping observations in which one goose chased another away from the corn used as bait. As the corn scattered in the vicinity of the trap became scarce the frequency of such aggressive-submissive interactions increased.

only one of his 117 threats (on individual birds) on his mate, Bb, despite the fact that special effort was made to establish the dominance relations within this pair; e.g., as many as 30 successive pieces of bread were tossed between them without the aggressive result that almost invariably followed this procedure when Br was near some other goose. Tolerance of one bird for its mate is apparently related to the degree of association permitted, and the birds assumed to be mates were the ones that in general kept company most often. Br and Bb tended to keep more closely together than did any of the other pairs of geese; this fact, together with an apparent antipathy of Pf for the pair, helps account for a large number of joint avoidances of Pf by this pair which were observed.

Another fact of interest is that each of the mated birds seemed to dominate much the same subordinates as did its mate; Lorenz (1935) has maintained that in flocks of geese the female assumes the social rank of the male to which she becomes mated. It can be seen from Table VI, furthermore, that the female, Bb, and Cr (of unknown sex) initiated few aggressive interactions, and were much less aggressive than were their respective mates. These birds belonged to the two most closely integrated pairs among the geese.

Frequency of threat reactions considered alone may not be a particularly good index to the intensity of dominance relations. For example, Bg was often threatened by Br and Bb because of the insistent tendency of Bg to associate with this pair. Bg was often driven off but persistently returned. Actually the other Barnacle Geese were tolerated less since they were usually attacked by Br at a much greater distance than he permitted to Bg, and so mere tabulation of the frequency of threats taken alone gives a false picture of the relationship. Bp and By received a relatively small number of threats, one reason being that they usually made off soon after bread was thrown to the geese or else they stayed to one side and did not compete very actively for the food. In contrast, Bu made little effort to avoid the other geese, actively competed for bread morsels, and was therefore often threatened by the other geese. Bp was a male Barnacle Goose of moderately high dominance status. It limped badly and initiated very few aggressive interactions, yet its subordinates were never seen to make any attempts to attack Bp.

From Table VI it may be seen that one intraspecies triangular arrangement existed with reference to the dominance relation, i.e., By dominated Bu, which dominated Bg, which in turn dominated By. An example of an interspecies triangle is the domination of Br by Pf, of Pf by Lu, and of Lu by Br. There was a rough association between body size and rank in the dominance hierarchy. The order of body size from largest to smallest was: Pink-foot, Barnacle, Lesser Canada, Cackling and Brant.

In summary, the non-breeding flock of geese moved freely about the enclosure and their grouping patterns were based on sex pairs and on larger subgroups. The more closely integrated pairs were characterized by a very low degree of intrapair aggression. In the feeding aggregation the degree of association of given individuals, other than sex pairs, was related to precedence according to the dominance hierarchy, and was also related to the species. In the non-feeding aggregations, subgroups other than sex pairs were associated with degree of similarity in plumage coloration of the different species and subspecies. A general factor causing aggregation in all the geese was the tendency to engage in the same type of activity at the same time.

One pair of very dominant Barnacle Geese attempted to breed and isolated itself from the other geese, which were aggressively kept away from the vicinity of the incubating female by the male and later from the vicinity of the young by both parents.

## Dominance Relations Observed in Other Species in the Zoological Park.

*In the Goose Enclosure.* Semi-wild Mallards and Black Ducks frequently flew into and out of the goose enclosure and were apparently dominated by all of the geese. Even the two Brants which were at the bottom of the goose dominance scale were each seen to threaten a Black Duck on separate occasions. Only very rarely did the ducks make any attempt to compete with the geese for food. The ducks themselves showed evidence of a dominance order, e.g., a female Mallard was seen to drive a Black Duck away from the feeding place one day.

Present in the enclosure were three Demoiselle Cranes, two of which were marked on the shoulders with green or red aniline dyes; they were designated G (green), R (red) and U (unmarked). They competed actively with each other and with the geese for the bread thrown into the enclosure. Cranes threatened other cranes or geese by advancing with partly opened bill, head low and slightly drawn back ready to jab, and at the same time they often uttered a harsh, rattling threat note. Crane G was at the top of the crane dominance order and was seen to dominate Crane R 86 times and Crane U 75 times. Crane R dominated Crane U 11 times.

*Dominance Relations in the Flying Cage.* The zoo has a very large flying cage, rectangular in shape, with an arched roof. It is approximately 150 feet long, 75 feet wide and 75 feet high. About half the floor area is occupied by a shallow cement-bottomed pool. A great variety of water birds were quartered in this cage. These birds were fed pieces of fish during the late afternoon; it was at this time that I sometimes observed

TABLE VII.

Dominance relations of certain wading birds of the southeastern United States as seen in a large flying cage. Dominators are listed to the left, subordinates are given in the row above.

| | American Egret | Reddish Egret | Roseate Spoonbill | Snowy Egret | Night Heron | White Ibis | Scarlet Ibis |
|---|---|---|---|---|---|---|---|
| *4 American Egret | 19 | 9 | 4 | 3 | 4 | 1 | 0 |
| 2 Reddish Egret | — | 2 | 3 | 0 | 4 | 2 | 1 |
| 4 Roseate Spoonbill | 5† | 2† | 4 | 9 | 0 | 5 | 3 |
| 3 Snowy Egret | — | — | — | 19 | 6 | 4 | 1 |
| 2 Black-crowned Night Heron | — | — | — | — | 0 | 0 | 0 |
| 6 White Ibis | — | — | — | — | — | 6 | 5 |
| 3 Scarlet Ibis | — | — | — | — | — | — | 0 |

* Number of individuals of each species.
† These interactions involved the same individual spoonbill.

them and recorded aggressive-submissive interactions.

Most of the aggressive-submissive interactions over the fish were observed in the wading birds, and a tabulation of the numbers of these interactions for species which occur in the southeastern United States revealed an interspecies dominance order (Table VII). The dominance order showed a rough parallel to the order of general size differences betwen the species. However, the dominance order did not strictly follow species lines. These birds were not marked but it was possible to distinguish certain individuals by size and plumage differences and thus to ascertain that in some cases dominance depended more on the individual characteristics than on the species characteristics. For example, the American and Reddish Egrets dominated two of the four Roseate Spoonbills, but the largest spoonbill dominated the American Egrets and at least one Reddish Egret as well as the other spoonbills.

Three to six individuals of each species of wader listed in Table VII were present in the cage, except for the Reddish Egrets and Black-crowned Night Herons of which there were two each. It is of special interest that most of the observed aggressive-submissive interactions of the American and Snowy Egrets were intraspecific. The same was true of the Water Turkeys of which there were some half dozen individuals present; 20 of their 27 aggressive-submissive interactions involved another Water Turkey, and definite signs of an intraspecies dominance order were observed.

Many other birds were present in the cage. As a rule the herons and ibises seemed to dominate the Laughing and Herring Gulls, Water Turkeys and Tree Ducks, although they did not often come into direct contact with these species.

One of the interesting general features of the aggressive behavior patterns of these water birds is that much the same pattern was used regardless of the species at which it was directed, e.g., a Snowy Egret would erect its crest, neck and body plumes in a sparring match whether its threat was directed against a Roseate Spoonbill, a Silver Gull or another Snowy Egret.

*Dominance Relations of Birds and Mammals in the "African Plains" Enclosure.* Various species of birds and mammals lived

TABLE VIII.

Dominance relations of certain African mammals and birds as observed in a large enclosure. Dominants listed in column to left, subordinates in row above. Figures refer to number of aggressive-submissive interactions.

| | Maribou | Blesbok | Ostrich | Imm. Nyala buck | Female Nyala |
|---|---|---|---|---|---|
| *1 Adult male Nyala | 6 | 3 | 7 | 35 | 11 |
| 2 Maribou Stork | — | 3 | 27 | 18 | 11 |
| 1 Adult male Blesbok | — | — | 0 | 5 | 7 |
| 1 Female Ostrich | — | — | — | 1 | 6 |
| 1 Immature male Nyala | — | — | — | — | 1 |
| 4 Female Nyala | — | — | — | — | 31 |

* Number of individuals.

TABLE IX.

Dominance relations between certain storks and cranes of the African Plains enclosure. Dominants listed to left, subordinates in upper row. Figures indicate number of aggressive-submissive interactions recorded.

| | Maribou | European Crane | Crowned Crane | Demoiselle Crane |
|---|---|---|---|---|
| *2 Maribou Stork | 0 | 1 | 3 | 1 |
| 2 European Crane | — | 0 | 8 | 30 |
| 4 Crowned Crane | — | — | 2 | 1 |
| 9 Demoiselle Crane | — | — | — | 2 |

* Number of individuals.

in the Zoological Park's large, moated African Plains enclosure. While the animals are at complete liberty within the confines of the area, species tended to remain more or less together. Dominance relations were recorded by noting and tabulating the number of aggressive-submissive reactions over introduced food, generally consisting of bits of bread or pieces of carrot which were thrown into the enclosure.

Table VIII reveals that a dominance order may involve both mammals and birds, and that some but not all individuals of one species may dominate individuals of another species. For example, the adult Nyala buck was at the top of the dominance order, whereas the immature Nyala buck and the female Nyalas were dominated by the Maribous, Blesbok and, less definitely, by the Ostrich.

Of special interest are the high degrees of aggressiveness of the Maribou Storks and the low degrees of aggressiveness of the female antelope. These several species of birds and mammals occupy overlapping ranges in Africa.

There were in addition to the mammals mentioned above four female Bushbuck and one female Reedbuck present in the African Plains enclosure most of the summer. These small antelope were dominated by the Maribous and Ostrich but they generally did not enter into active and aggressive food competition with the other species of antelope and few of their dominance relations to these were established.

Table IX illustrates the dominance relations of the storks and cranes of the African Plains enclosure. The European Crane and Demoiselle Crane both breed in Europe and may winter in northeast Africa. The ranges of the Maribou Stork and Crowned Crane are more southerly but extend northward into northeast Africa.

This dominance order roughly parallels the size of the birds. The Maribous have very large beaks which reinforce their aggressive disposition. The small Demoiselle Cranes generally avoided the Maribous, so practically no aggressive-submissive interactions were recorded between these two species. It should also be noted that the two species at the top of the dominance order, i.e., the Maribous and European Cranes, each consisted in this instance of a closely integrated pair of individuals.

Early in the summer the European Cranes nested and hatched out two young within the enclosure. While one parent sat on the nest the other would stand guard nearby and try to keep all other birds and mammals away from the vicinity of the nest. The female Ostrich was frequently chased 20 or 30 feet or more. When the adult Nyala buck grazed close to the nest the male European Crane placed himself between his mate and the antelope and with his beak pointed skyward indicated his disturbance by repeated loud trumpeting. He did the same when the Maribous approached. They did not retreat, and perhaps his inability to dominate them was fatal to one of the young, since the Maribous were later seen pulling at its dead body, which one of them swallowed. When keepers entered the enclosure to remove the remaining young bird to safety, both parent cranes feigned injury. This behavior pattern had not been seen when the safety of the nest or young was previously threatened by other birds or mammals living in the enclosure.

*Dominance Relations of Certain Mammals in Other Large Enclosures.* The importance of dominance for precedence to mates among antelope was well seen in the case of an adult male Indian Blackbuck which spent much of its time keeping six or seven immature bucks away from a sizable herd of females. This particular buck had killed his predecessor, as well as some of the immature males.

Mr. Irwin Katz (1949) was able to demonstrate the existence of a dominance order in a small herd of Barbary Sheep in a large outdoor enclosure in the Zoological Park. The males dominated the females and young; the males are heavier and have much larger horns than do the females.

No detailed study of the dominance relations of any of the carnivorous mammals at the New York Zoological Park was attempted. Cooper (1942) observed a dominance hierarchy among lions in a large outdoor enclosure at a lion farm in California. Among piscivorous mammals a dominance hierarchy has been described for captive Bottle-nose

Dolphins at the Marine Studios in Florida (McBride and Hebb, 1948).

*Mode of Expression of Aggressive Behavior.* Considerable structural adaptations to special conditions may exist without greatly altering certain patterns of aggressive behavior; thus biting or threatening with the beak was observed in such birds as geese, herons, spoonbills and ibis with very diverse beaks. Many birds retain the old reptilian pattern of hissing. At the New York Zoological Park or in other zoos and localities the following birds were heard to hiss either as a threat against other birds or as a defense against human beings: Ostrich, Rhea, Jabiru Stork, White Stork, European Bittern, Graylag Goose, Mute Swan, Ring-necked Pheasant, various vultures, young domestic pigeons and young Wood Pigeons. Others have recorded hissing in comparable stimulus situations for the following: Gentoo Penguin (Murphy, 1936), Cormorant, Capercaillie, Red Grouse, Common Partridge, Black Guillemot, Scops Owl, Barn Owl, Hoopoe (young), Wryneck and European Cuckoo (Witherby, et al., 1943). Interestingly enough, young Homing Pigeons in the nest, but not the parent, would hiss at my intruding finger. Passerine birds as a group have highly developed voices, and records of hissing seem to be rare in this order. However, the Blue Tit is said to hiss on the nest when disturbed (Coward and Blyton, 1941). The White Stork is practically voiceless, but uses both hissing and bill clattering as a threat. Among mammals, the primitive Platypus is said to hiss occasionally under stress (Holmes, 1939).

Several species of antelopes were observed to interlock their horns in sparring for an opening, and it is possible that the peculiar shape of the horns of many species is in part to be explained by evolution of species-specific interlocking patterns. The horns of the White-tailed Gnu curve forward, those of the Brindled Gnu sideways, and the behavior patterns when these animals would hook the bars of their cages differed in corresponding fashion. The fixity of the behavior pattern that corresponds to a special type of horn was demonstrated repeatedly by a Beisa Antelope of aggressive disposition in which the very long horns had been sawed off near their base. When its neck was touched lightly it would at once go through the complex stereotyped motion of thrusting the horns. It never made any effort to butt with its head, but apparently depended on the horns which it no longer had.

In summary, dominance hierarchies based on aggressive behavior were observed in species of a wide variety of bodily conformations and habitat types. These animals were maintained in relatively large enclosures. Intraspecies dominance hierarchies were observed by the author for Black-footed Penguins, various geese, Demoiselle Crane, White-tailed Deer and Nyala Antelope; by others for Barbary Sheep, Lions and Bottle-nose Dolphins. Interspecies dominance hierarchies were observed for various large wading birds, geese and ducks; the same hierarchy may include both birds and mammals, as was observed for various African species.

The pattern of aggressiveness varies to some extent with special structures, as seen in the correlation of type of horn with a given type of fighting pattern in certain antelopes. The occurrence of reptile-like hissing in many orders of birds as well as in some mammals indicates a conservative element in the evolution of aggressive behavior patterns.

## Dominance Hierarchies in Unconfined Birds and Mammals.

On the basis of observation revealing the general occurrence of dominance hierarchies in confined animals, an investigation was made of the literature concerning the occurrence of such hierarchies in unconfined animals. Some of the earlier results of this effort have been reviewed elsewhere (Collias, 1944).

*Intraspecies* dominance hierarchies have been described for wild or unconfined birds in the following species: breeding groups of Sage Grouse on the dry plains of the western United States (Scott, 1942); Wild Turkeys in mixed hardwood and coniferous forest (Mosby and Handley, 1943); Ring-necked Pheasants wintering in a marsh overgrown with vegetation, (Collias and Taber, 1948); California Valley Quail along wooded streams bordering farmlands (Howard and Emlen, 1942); and a number of perching birds of woodland, farm, village and garden, including the very sociable Jackdaw (Lorenz, 1931) and winter flocks of Black-capped Chickadees (Odum, 1941, 1942), Blue Tits (Colquhoun, 1942), Tree Sparrows and Slate-colored Juncos (Sabine, 1949). In the breeding season most species of birds establish territories which they defend usually with considerable success from other members of their species, but Mrs. Nice (1943, p. 93) and Armstrong (1947, p. 285) cite many intraspecies instances, from penguins to passerines, of individual intruders dominating or even evicting other individuals from the territory of the dominated bird.

Mammals in which intraspecies dominance hierarchies under free-ranging conditions have been recorded include large herbivores like the zebra on the plains of Africa, (Alverdes, 1935), Mule Deer bucks in the coniferous mountain forests of California (Dixon, 1934), Red Deer in a Scottish forest (Darling, 1937); large carnivores like the Wolves and Grizzly Bears of Mount McKinley in Alaska (Murie, 1944; p. 28, p. 202); various small gnawing mammals such as the Wild Rabbit in England (Southern, 1948), the Golden-mantled Ground Squirrel and certain Chipmunks of the western United States (Gordon, 1940); and such primates as Gibbons (Carpenter, 1940), Rhesus Monkeys

(Carpenter, 1942), and Chacma Baboons (Zuckerman, 1932). Howler Monkeys probably have a dominance social gradient of low slope (Carpenter, 1942b).

*Interspecies* dominance orders have been recorded, usually somewhat incidentally, for various water and land birds. Among the ducks and geese on a park lagoon in Chicago (Jenkins, 1944) the following order was observed: a family of Blue Geese, Canada Geese, another pair of Blue Geese, Snow Geese, Mallards, Wood Ducks and Scaups. In this case, however, the adult Blue Geese and the Snow Geese were wing-clipped. Roughly, this is the order of size differences, except that the closely organized family of Blue Geese was able to dominate the much larger, more numerous and relatively unorganized Canada Geese.

The Ringed Penguin exercises aggressive dominance over the Adelie and the Gentoo Penguins in places in the Antarctic where these three species nest together (Murphy, 1936, p. 408). In the tropical rain forest of the Panama Canal Zone the aggressive little Striped Flycatcher has been seen to evict the much larger Oropendula from its nest, which the flycatcher may then appropriate for its own use (Chapman, 1929, p. 111-118). In the tropical forest of British Guiana, Beebe (1917) observed that hummingbirds feeding at flowering trees may attack other species of hummers, centering their attack more on some species than on others (p. 115); and he also noted that King Vultures always took precedence to carrion over other local species of vultures, such as the Yellow-head Vulture (p. 110).

The existence of interspecies dominance orders among birds that inhabit our woodlands, woodland borders, farms, villages and gardens is rather widely known because of the prevalence of *winter* feeding stations. In 1929 Mrs. Nice published her observations of such a hierarchy among certain winter birds in the central United States. In general, the order judged from precedence to food and aggressive interactions was as follows: Mockingbird, Cardinal, Harris Sparrow, Lincoln Sparrow, English Sparrow, and Field Sparrow. Sabine (1949) has recently described an interspecies dominance order in which different individual Juncos and Tree Sparrows were arranged in a triangular relationship with respect to each other. Colquhoun (1942) in Great Britain has noted an interspecies dominance order at a winter feeding hopper, including nuthatches and various species of titmice.

During the *spring* of 1948, at a pile of corn in a marsh near Madison, Wisconsin, it was observed that the male Red-winged Blackbird, which had established his territory at that spot, dominated the Song Sparrow which also had his territory in about the same place. Both of these birds with their mates eventually fledged young. They dominated the local Swamp Sparrows, a Catbird and a migrant White-Throated Sparrow. Most of these contacts were observed repeatedly (previously unpubl.).

Small passerine birds may also show dominance relations at a feeding station during the *summer*. Dr. William Beebe reports the following observations:

"A continual daily supply of sunflower and other seeds attracted birds to a flat rock in a garden near Wilmington, south central Vermont. From July 22nd to 30th a few notes were made on peck dominance or tyrannization among several species and varying ages. . . . The general order of dominance, checked and rechecked day after day, was as follows: 1- Indigo Bunting, 2- Adult male Purple Finches, 3- Juncos, 4- adult White-throated Sparrows, 5- Song Sparrows, 6- White-crowned Sparrows, 7- Immature White-throated Sparrows, 8- Immature Purple Finches, 9- Chipping Sparrows.

". . . Neither size nor abundance of individuals had anything to do with this order of tolerance. If we consider the sequence from dominant to submissive as 1 to 9, we find the corresponding order in respect to size, from the smallest up, to be: 9, 1, 3, 2, 8, 5, 4, 7 and 6. The same scale in abundance from rarest is: 1, 6, 4, 4, 9, 5, 3, 7 and 8.

"Occasional temporary shifts in dominance order were occasioned by the individuality of some single bird. One Song Sparrow fought steadily for his rights with all above him, and one immature Purple Finch had to be physically assaulted before he would give way."

In general interspecific dominance hierarchies seem to parallel gross size, but this rule is subject to some marked exceptions. For example, Kingbirds will go far from their nest site to attack a much larger bird like a Crow or Red-tailed Hawk (Davis, 1941), and small birds may gang up together on an owl or cat.

There is, of course, nothing absolute about any of these various interspecies dominance hierarchies as given here. Apart from their existence, it is of interest that so much variation results from differences in age, sex, territorial relations and other individual differences.

In summary, dominance hierarchies based on aggressive behavior have been observed in unconfined birds and mammals of a wide variety of species and habitats. *Intraspecies* hierarchies have been observed in land and water birds, and among fish-eating, carrion-feeding, seed-eating and insectivorous birds. Among mammals intraspecies dominance hierarchies have been observed in forest and grassland, herbivorous and carnivorous, cursorial and arboreal types. *Interspecies* dominance hierarchies have also been observed for birds of a wide range of habitat types as well as for those from diverse geographic localities, including species from polar and equatorial regions, temperate woodland and tropical jungle, desert and the ocean. Interspecies hierarchies have been observed dur-

ing the breeding and the non-breeding seasons for passerine birds.

Such observations, although not always as detailed as one would like, indicate that the *existence* of dominance hierarchies based on aggressiveness is one of the more general principles of social life among birds and mammals, and therefore one of the general problems which the different species of birds or mammals must face wherever they live together in a community.

## Some General Comparisons and Conclusions.

Field and laboratory studies exert a reciprocal influence. Field studies provide a basic orientation but are often difficult and in such cases fruitful working hypotheses may be derived from laboratory studies. Thus the present study indicates that a fruitful field endeavor would be the detailed observation and study of the dominance relations within and between various species of wild birds on a pond or of the wild animals at an African waterhole.

The evidence which has been presented indicates that dominance hierarchies based on aggressive behavior are of widespread occurrence in different ecological types of birds and mammals in the field and in captivity.

Dominance hierarchies, like territorial relations, are also of widespread occurrence from a phylogenetic point of view. Both types of dominance patterns have been recorded in all the classes of living vertebrates, from the bony fishes to mammals, except for the Amphibia (Collias, 1944). Recently, Dr. A. F. J. Portielje of the Amsterdam Zoological Garden informed me that he had observed vigorous and persistent fighting between individuals of the Japanese Giant Salamander (*Megalobatrachus japonica*) in the aquarium of this zoo. This salamander is relatively primitive compared to other living amphibia and the occurrence of aggressive behavior in some of the more primitive members of various classes of living vertebrates makes it probable that such behavior is a primitive vertebrate attribute; it has been recorded for the Lake Lamprey among jawless forms (Noble, 1938), for *Amia* (Reighard, 1903) among the bony fishes, for *Sphenodon* (Gadow, 1901) among the reptiles, and for *Ornithorhynchus* (Burrell, 1927, p. 92, 166-167; Fleay, 1944, p. 74) among mammals.

Aggressive behavior, apart from predator-prey relations, has also been described for members of such important invertebrate groups as cephalopods (cf. Tinbergen, 1948), decapod crustaceans (Allee and Douglis, 1945; Douglis, 1946), spiders (Bristowe, p. 498-502, 1941), and insects including ants, bees, wasps (Wheeler, 1939; Pari, 1948), chalcids, butterflies, various dipterous flies, crickets, grasshoppers, stag beetles (Richards, 1927) and Hercules beetles (Beebe, 1947). Aggressiveness among invertebrates may be expressed in relation to dominance hierarchies, territorialism or sex competition. These phenomena are therefore not restricted to vertebrates, but the present evidence indicates that this is a rich field for the investigator of invertebrate behavior (Allee, 1950).

Aggressive behavior is most likely to be displayed when one animal invades the territory of another, or in the case of dominance hierarchies, between individuals in which the dominance relationship is unsettled. Such cases of unstable dominance relations were observed within every group studied at the New York Zoological Park, but on the whole were rare. Yerkes (1943) has written that among captive Chimpanzees contests for social supremacy may be brief and decisive, or long continued and indeterminate, particularly in the case of evenly matched contestants (p. 48).

The tendency to form aggregations is even more widespread among both vertebrates and invertebrates than is the phenomenon of aggressive behavior (Allee, 1931, 1945; Collias, 1944). This has raised the problem of the nature of the relationship between these two apparently antagonistic forms of behavior. One solution providing for increased group coherence has been the increase of intragroup tolerance associated with a decrease of individual aggressiveness, as in the case of the female Nyala Antelope. The more aggressive and more loosely aggregated does of the White-tailed Deer provide a contrasting case. A related solution has been increase in specific intragroup tolerance associated with extragroup aggressiveness as in the sex pairs of birds such as penguins and geese. Another common type of solution, particularly among birds, has been the territorial isolation of the breeding pair from the rest of the group.

In general, the birds that held territories were also high in the dominance hierarchy, for example, the Barnacle pair, Br and Bb on the goose pond, Pairs 1, 2 and 3 in the penguin colony, and the European Cranes in the African Plains enclosure. These same pairs were relatively well integrated compared to other pairs of birds in the same enclosures. However, they were also relatively heavy in body weight, so it is not clear which of the correlations are causal in nature. Lack (1940) placed two pairs of British Robins and two pairs of Chaffinches in a fair-sized aviary; only the dominant pair of each species bred.

The effective protection and welfare of the young may require a rather high degree of dominance by the parents. Thus, inability of a parent to dominate an aggressor resulted in attacks on the young, as described for the penguins and Barnacle Geese. The same thing was also seen for an Indian Peafowl driven from her young one by a Marabou Stork. Katz (1949) observed in the Barbary Sheep that a ewe of low dominance status was often excluded, together with her lamb, from the food place for prolonged periods of time.

Simultaneous attack on a common enemy possibly helps integrate a group to some extent. Such cooperative aggression by two individuals of the same species on a third animal was observed for pairs of Black-footed Penguins, Roseate Spoonbills, Snowy Egrets, Australian Black-backed Pelicans, Maribou Storks and Himalayan Tahrs. Intraspecies aggressive behavior by groups above the level of the sex pair acting more or less as a unit has been recorded for a few species of birds and a few species of non-primate mammals, but seems to be particularly characteristic of the higher primates (cf. Collias, 1944).

Various other factors serve to increase the aggegating tendency under different conditions and have been reviewed in detail elsewhere (Collias, in press).

A little evidence gathered in this study supports the general idea that competition is more intense within than between species. Thus the American Egrets, the Snowy Egrets and the Water Turkeys, although caged with many other species of birds, were observed in aggressive encounters with members of their own species much more often than with members of other species. According to Howard (1920), territorial encounters in birds seem to be more frequent in the same or related species. Carpenter (1942b) has made a quite similar case for primates: "I have seen howlers feeding in the same trees with capuchin monkeys, gibbons feeding in the same tree with langurs. I have never observed organized groups of the same species *peacefully* associated. One may generalize by saying that among monkey and ape societies, intra-species competitions and group antagonisms are much stronger than between groups of different species or genera."

## Summary.


A. Dominance and grouping patterns were studied in small groups of selected mammals and birds kept in large enclosures at the New York Zoological Park of the New York Zoological Society.

1. A group of White-tailed Deer consisting of 6 does and 3 bucks had a dominance hierarchy reinforced by frequent aggressive-submissive interactions. In association with their aggressive nature the individuals were often scattered widely about the enclosure.
2. A group of 5 female Nyala Antelope, which normally showed no apparent aggressive interactions, moved about usually as a compact herd unit. An adult buck accompanied the females and generally kept a smaller, immature buck at some distance from the females.
3. A colony of 14 penguins (mainly Black-footed Penguins) were organized chiefly on the basis of individual pair territories. However, a dominance hierarchy existed on neutral ground.
4. A small flock of several species of geese had a dominance hierarchy with specific tolerances and subgroups based in large part on sex pairs within the larger flock.

B. Competition for food, and breeding success were related to the dominance hierarchies observed.

1. By restricting the unaggressive female Nyala Antelope to short rations for two days an unstable dominance hierarchy was made evident or developed.
2. By introducing specific pieces of food for which the geese competed, the number of observed dominance-submissive interactions was increased more than ten-fold.
3. Successful breeding was associated with high social rank in the penguins; and failure of a dominant pair of Barnacle Geese to breed successfully was apparently due to their inability to dominate one other goose in the enclosure.

C. Interspecies dominance hierarchies were found to exist among various water birds, as well as among certain species of birds and mammals from the African veldt. In addition to general size of species, rank in these hierarchies varied with age, sex, territorial relations and other aspects of individuality. In some of the water birds aggressive-submissive encounters occurred at a higher rate within the species than between species.

D. Tendency to aggregate was associated with degree of difference in coloration and pattern of plumage in the case of different species of geese and pelicans and also with the tendency for various individuals of the same or related species to engage in the same type of activity at the same time, in all groups studied.

E. Comparison of the results obtained at the Zoological Park with recorded instances of grouping patterns and dominance hierarchies among various species in nature indicates that the results of these observations in a zoo to a certain extent will have applicability to natural situations and should provide favorable working hypotheses for field studies.


## Bibliography.


Allee, W. C.

1931. Animal aggregations: a study in general sociology. Chicago: University of Chicago Press. 431 pp.

1945. Human conflict and cooperation: the biological background. Chap. 20, pp. 321-367, of "Approaches to National Unity". Fifth Symposium of the conference on science, philosophy, and religion. Edited by L. Bryson, L. Finkelstein, & R. M. MacIver. New York: Harper & Bros.

1950. Extrapolation in comparative sociology. *Scientia*, 43: 135-142.

ALLEE, W. C. & DOUGLIS, MARJORIE B.
1945. A dominance order in the hermit crab, *Pagurus longicarpus*. *Ecology*, 26: 411-412.

ALVERDES, F.
1935. The behavior of mammalian herds and packs. A chapter in Murchison's Handbook of Social Psychology. Worcester, Mass.: Clark Univ. Press.

AMERICAN ORNITHOLOGISTS' UNION.
1931. Check-list of North American Birds. 4th ed. 526 pp. Lancaster, Pa.: American Ornithologists' Union.

ARMSTRONG, EDWARD A.
1947. Bird display and behaviour. London: Lindsay Drummond, 431 pp.

BEEBE, WILLIAM.
1917. Tropical wild life in British Guiana. Vol. I, Part I. 290 pp.
1947. Notes on the Hercules beetle, *Dynastes hercules* (Linn.), at Rancho Grande, Venezuela, with special reference to combat behavior. *Zoologica*, 32: 109-116: 4 pls.

BRISTOWE, WILLIAM SYER.
1941. The comity of spiders. London: Bernard Quaritch, Ltd. 560 pp.

BURRELL, HARRY.
1927. The Platypus. Sydney, Australia: Angus and Robertson Ltd. 227 pp.

CARPENTER, C. R.
1940. A field study in Siam of the behavior and social relations of the gibbon (*Hylobates lar*). *Comp. Psychol. Monog.*, 10(2): 1-168.
1942a. Sexual behavior of free ranging rhesus monkeys (*Macaca mulatta*). 2. Periodicity of estrus, homosexual, autoerotic and nonconformist behavior. *Jour. Comp. Psychol.*, 33: 143-162.
1942b. Societies of monkeys and apes. *Biol. Symp.*, VIII: 177-204.

CHAPMAN, FRANK M.
1929. My tropical air castle. Nature studies in Panama. New York: D. Appleton & Co. 417 pp.

COLLIAS, N. E.
1944. Aggressive behavior among vertebrate animals. *Physiological Zool.*, 17: 83-123.
—— Social life and the individual among vertebrate animals. (in press). Annals New York Academy of Sciences.

COLLIAS, NICHOLAS E. AND TABER, RICHARD D.
1948. Grouping and dominance relations among wild Ring-necked Pheasants. *Anat. Rec.* (Suppl.), 101: 44-45.

COLQUHOUN, M. K.
1942. Notes on the social behaviour of blue tits. *Brit. Birds*, 35: 234-240.

COOPER, J. B.
1942. An exploratory study on African Lions. *Comp. Psychol. Monog.*, 17(7): 1-48.

COWARD, T. A. AND BLYTON, ENID.
1941. Birds of the Wayside and Woodland. London and New York: Frederick Warne and Co.

DARLING, F. F.
1937. A herd of red deer. London: Oxford Univ. Press. 215 pp.

DAVIS, DAVID E.
1941. The belligerency of the Kingbird. *Wilson Bull.*, 53: 157-168.

DIXON, JOSEPH S.
1934. A study of the life history and food habits of the mule deer in California. *Calif. Fish and Game Bull.*, Vol. 20, nos. 3 & 4. 146 pp.

DOUGLIS, MARJORIE B.
1946. Interspecies relationships between certain crustaceans. *Anat. Rec.* (Suppl.), 96: 57-58.

FITZSIMONS, F. W.
1920. The natural history of South Africa. Vol. 3, 278 pp. London: Longmans, Green & Co.

FLEAY, D.
1944. Observations on the breeding of the Platypus in captivity. *Victorian Naturalist*, 61: 74-78.

GADOW, HANS.
1901. Amphibia and reptiles. Cambridge Natural History. Vol. 8, 668 pp. London and New York: Macmillan and Co.

GORDON, K.
1940. Territorial behavior and social dominance among Sciuridae. *Jour. Mammalogy*, 17: 171-172.

HOLMES, CHARLES H.
1939. Australia's patchwork creature, the Platypus. *Nat. Geog. Mag.*, 76:273-282.

HOWARD, H. E.
1920. Territory in bird life. London: John Murray. 308 pp.

HOWARD, W. E. AND EMLEN, J. T.
1942. Intercovey social relationships of the Valley Quail. *Wilson Bull.*, 54:162-170.

JENKINS, D.
1944. Territory as a result of despotism and social organization as shown by geese. *Auk*, 61:30-47.

KATZ, IRWIN.
1949. Behavioral interactions in a herd of Barbary Sheep (*Ammotragus lervia*). *Zoologica*, 34:9-18.

KEARTON, CHERRY.
1930. The island of penguins. New York. 223 pp.

LACK, D.
1940. Observations on captive robins. *Brit. Birds*, 33:232-270.

LORENZ, K.
1931. Beiträge zur Ethologie sozialer Corviden. *Jour. f. Ornith.*, 79:67-127.

1935. Der Kumpan in der Umwelt des Vögels. *Jour. f. Ornith.*, 83: 137-213, 289-413.

MOSBY, HENRY S. AND HANDLEY, CHARLES O.
1943. The wild turkey in Virginia. Richmond: Pittman-Robertson Projects. Division of Game. 281 pp.

MURIE, ADOLPH.
1944. The wolves of Mount McKinley. Fauna of the National Parks of the United States. Fauna Series No. 5. 238 pp.

MURPHY, ROBERT CUSHMAN.
1936. Oceanic birds of South America. Vol. I. Amer. Mus. Nat. Hist., N. Y. 640 pp. 2 vols.

NICE, MARGARET MORSE.
1943. Studies in the life history of the Song Sparrow. 2. The behavior of the Song Sparrow and other Passerines. *Trans. Linn. Soc. N. Y.*, 6: 1-329.

NOBLE, G. K.
1938. Sexual selection among fishes. *Biol. Rev.*, 13: 133-158.

ODUM, E. P.
1941. Annual cycle of the black-capped chickadee. I. *Auk*, 58: 314-333.
1942. Annual cycle of the black-capped chickadee. III. *Ibid.*, 59: 499-531.

PARDI, L.
1948. Dominance order in *Polistes* wasps. *Physiological Zool.*, 21: 1-13.

REIGHARD, JACOB.
1903. The natural history of *Amia calva* Linnaeus. Mark Anniversary vol., pp. 57-109. New York: Henry Holt & Co.

RICHARDS, O. W.
1927. Sexual selection and allied problems in the insects. *Biological Reviews*, 2: 298-364.

ROBERTS, BRIAN.
1940. The breeding behavior of penguins with special reference to *Pygoscelis papua* (Forster). British Graham Land Expedition, 1934-37. *Scientific Reports*, 1(3): 195-254. British Mus. Nat. Hist.

SABINE, WINIFRED S.
1949. Dominance in winter flocks of Juncos and Tree Sparrows. *Physiological Zool.*, 22: 64-85.

SETON, ERNEST THOMPSON.
1929. Lives of game animals. Garden City, N. Y.: Doubleday, Doran & Co., Inc. Vol. 3, Pt. 1. Hoofed Animals. 412 pp.

SCOTT, J. W.
1942. Mating behavior of the sage grouse. *Auk*, 59: 477-498.

SOUTHERN, H. N.
1948. Sexual and aggressive behavior of the Wild Rabbit. *Behaviour*, 1(3-4): 173-194.

TINBERGEN, N.
1948. Social releasers and the experimental method required for their study. *Wilson Bull.*, 60: 6-51.

WHEELER, W. M.
1939. Essays in Philosophical Biology. Cambridge, Mass.: Harvard Univ. Press, 261 pp.

WITHERBY, H. F., et al.
1943. The handbook of British birds. V vols. London: H. F. & G. Witherby, Ltd.

YERKES, ROBERT M.
1943. Chimpanzees. A laboratory colony. New Haven: Yale University Press. 321 pp.

ZUCKERMAN, S.
1932. The social life of monkeys and apes. New York: Harcourt, Brace & Co., 356 pp.

# 7.

# Fishes that Live as Inquilines (Lodgers) in Sponges.

E. W. Gudger.
*American Museum of Natural History.*

(Text-figures 1 & 2).

## Introduction.

The living habits of fishes are extraordinarily diversified and are interesting in like degree. Among inanimate objects, they seek protection in crevices in rocks, in holes in and under banks of streams (some burrowing fishes make the holes which they inhabit), under stumps, roots—projecting bodies of any kind in the water—and in aquatic plant growths, both marine and fresh-water. And recently it was noted that when a floating log was brought ashore, out came a catfish. All this, of course, is probably for protection from enemies.

But among the most interesting living habits of fishes are those in which they seek protection by associating as inquilines (Latin, *inquilinus*, a lodger) with the lower invertebrate water-dwellers—some of them normally fish-eaters. Thus the little *Nomeus* finds safety in associating with the very dangerous Portuguese Man-of-War, *Physalia*, with its long, trailing tentacles beset with thousands of the most virulent poison cells known in any hydroid. Then various small fishes live under the umbrellas of large jellyfishes, protected from their enemies by the poison cells in the tentacles hanging from the outer edge of each umbrella. Again, certain small pomacentrid fishes live unhurt amid the poison-cell-laden tentacles of giant sea anemones found from the head of the Red Sea to the Fiji Islands, and from the South China Sea to the waters around northern Australia.

This last may be set down as a case of symbiosis. When pursued by other (predator) fishes, the little pomacentrids flee to their protectors, and the prosecutors following them meet their doom and are eaten by the protective anemones—the scraps falling to the little enticers. One student of this association of huge anemones and little fishes at the head of the Red Sea is convinced that the little fishes act purposely in leading to their anemone hosts the larger fishes.

In 1914, at the Marquesas Atoll, 20 miles west of Key West, I found a little *Apogonichthys* lodging in the mantle cavity of a large univalve mollusk (the conch, *Strombus*). Later I found that this had previously been recorded from the Bahamas, where the phenomenon is now well known. For an account of this find, see Gudger, 1927. This fish is also known as a sponge inquiline, as will be shown later.

Then the little eel-like pearlfish, *Fierasfer*, has been found sojourning in the mantle cavity of the pearl oyster, *Meleagrina*, and in the posterior digestive tract of holothurians ("sea cucumbers").

That crustaceans live in the lowly sponges as inquilines has been recorded since 1850, but that fishes indulge in the practice has been known for but a comparatively short time, not farther back than 1917—so far as this study has shown. At least, no such titles were found in a check-up of G. C. J. Vosmaer's "Bibliography of Sponges, 1551-1913." Hence the accounts of fish-sponge inquilinism begin with 1917.

## Fishes that Live in Sponges in the Western Central Atlantic.

So far as this search has revealed, this curious form of inquilinism of fish-in-sponge seems to have been reported only from the central western Atlantic Ocean. It surely must occur in the warmer parts of the Pacific and Indian Oceans also. That there are no reports from these oceans can only mean that the habit has not been recorded from them because it has not been looked for.

The accounts of the discoveries of fish-sponge inquilinism will now be presented in the chronological order of discovery by genus and species. Where there is more than one report of a species and where two species of a genus are found to be inquilines, the chronological order of recording each species will be followed.

### ***Evermannichthys spongicola*** Hubbs, 1923.

I (1)—*Garmannia spongicola*—Radcliffe, 1917.[1]

The history of the first known record of fishes living in sponges is as follows:

In the summer of 1917, the U. S. Fisheries Steamer *Fish Hawk* came to the Fisheries Laboratory at Beaufort, N. C., to do some experimental trawling. On August 1, she made an exploratory trip to the fishing grounds about 20 miles south by west of

[1] The Roman numerals indicate the chronological order of discovery of sponge inquilines by genera. The Arabic numerals in parentheses (1) indicate the number of reports of inquilinism by the species.

Beaufort Inlet. Here in about 15 fathoms she put out a beam trawl on hard bottom with corals and sponges. Among the spoils brought up was a large cup-shaped sponge, concave on top and 61 cm. in diameter. From its deep cavity there were taken six little gobies 24-28 mm. long. On August 11, another trip was made. This time the trawl brought up a sponge 45.7 cm. in diameter at the top and 53.3 cm. high. It, too, was cup-shaped. From this sponge were extracted 15 little gobies varying from 20 to 31 mm. in length. Both sponges were pretty heavily inhabited by these little fish.

These gobies were new to science and to them Lewis Radcliffe, at that time director of the U. S. Fisheries Laboratory at Beaufort, gave the name *Garmannia spongicola*—Garman's sponge-dwelling goby. These were named for Dr. Samuel Garman, ichthyologist of the Museum of Comparative Zoology in Cambridge, Massachusetts.

(2)—Later, Radcliffe found in the collections of the Bureau of Fisheries five unidentified gobies ranging from 17 to 27 mm. in length. These had been taken on January 13, 1913, off the Anclote Keys near Tarpon Springs, west coast of Florida, from a large sponge similar to those noted above. When examined, these little gobies were found to be identical with the above, and are so noted at the end of Radcliffe's article (1917). Presumably the members of this species normally lodge in sponges, wandering away in search of food, but coming "home" when they have fed or when molested.

In 1923, Hubbs, after studying Radcliffe's gobies and after working over other sponge-dwelling gobies collected by Metzelaar at Curaçao, Lesser Antilles, and named *Evermannichthys spongicola*, assigned the generic name *Evermannichthys* to Radcliffe's gobies. This genus is named in honor of Dr. B. W. Evermann, an outstanding student of American fishes. So the generic name of these little gobies is that at the head of this section. Metzelaar's work will now be noted.

***Evermannichthys metzelaari*** Hubbs, 1923.

II (1)—*Evermannichthys spongicola*—Metzelaar, 1919.

In 1919 Metzelaar described from many specimens this small goby (up to 26 mm. in length) found off Curaçao "in sponges . . . where the fish lives together with its congener, *Gobiosoma multifasciatum*." It should be noted that Metzelaar is the first to find two different but related genera of fishes living in the same sponge. Later, three such unrelated co-dwellers will be registered. As noted earlier, Hubbs in 1923 changed the specific name of this fish as recorded above.

(2)—In 1922, Metzelaar made a second finding of this same goby "living in sponges" in another locality off Curaçao, Dutch West Indies.

The next findings of the little Evermann-Metzelaar gobies are far away in time and space from the preceding.

(3)—In 1928, Beebe & Tee-Van, in their intensive study of the fishes of Port-au-Prince Bay, Haiti, say of these little gobies (*Evermannichthys metzelaari*) that "Seven of these remarkable fish were taken from the galleries of enormous sponges, where they lived in company with snapping shrimps and small crabs." And of the large pectoral fins of these little (19 mm. and smaller) fish, they note that: ". . . the webs are torn to ribbons, mostly by attrition on the silicious sponge substance"—as the little gobies make their way into and out of the sponges.

The careful observations of these veteran observers are what the reader has wished for with regard to the habits of these fishes. More of their observations will follow later for these and for other sponge-dwellers.

Two other records of the Evermann-Metzelaar goby have come to hand and from another quite distant locality:

(4)—In 1932, Pearse, in listing the denizens of a large vase-shaped sponge taken and dissected at Tortugas, Florida, records "a fish, *Evermannichthys metzelaari*." It is strange that, in all his work with sponges at the Tortugas Laboratory, Pearse found but a single inquiline fish.

(5)—Last of all, however, in 1941, "The Fishes of Tortugas, Florida" was published. In it, Longley & Hildebrand say (p. 229) of *Evermannichthys metzelaari*—"Common at Tortugas in loggerhead sponges." The largest of five in one sponge was 27 mm. long. This is from Longley's notes.

The five records above give quite an extensive distribution to Metzelaar's *Evermannichthys*. It is recorded from Curaçao, Dutch West Indies, Port-au-Prince Bay in Haiti, and from the Tortugas. And there is every reason to expect that it will be found in sponges throughout the whole Caribbean-Gulf region.

Having brought together in chronological order all the Evermann-Metzelaar gobies to show their wide distribution, we now return to the discovery by this Dutch ichthyologist of a new genus of sponge-dwellers.

III (1)—***Gobiosoma multifasciatum***—Metzelaar, 1919.

In 1919, Metzelaar recorded several specimens of this fish (length up to 23 mm.) from Curaçao, Dutch West Indies, all "living in sponges." And three years later our Dutch ichthyologist records another species of this genus—as will now be seen.

IV (1)—***Gobiosoma horsti***—Metzelaar, 1922.

Last of all Metzelaar's sponge-dwellers from the Lesser Antilles is the goby listed above. Of it he merely says—"Two specimens of 55 mm. from a sponge, Caracas Bay." No details are given, but in the same article he adds two more sponge-dwellers to his list—as will be noted further on.

(2)——Beebe & Tee-Van (1928) say of their specimens of this goby in Port-au-

Prince Bay, Haiti, that—"Almost all the Haitian fish were taken from tall tubular sponges" on reefs 12-15 feet down. However, "the gobies are not confined to the sponges, but came out during the daylight and were often seen resting on the bottom." But they found them in about half of these tall tubular sponges on the reef.

V (1)—**Garmannia rubra**—Metzelaar, 1922.

Metzelaar merely notes of this little goby —"Many specimens from sponges in Curaçao Bay." One wishes for details, particularly the kind of sponge in which they were found.

VI (1)—**Garmannia binghami**—Parr, 1927.

The Third Oceanographic Expedition of Mr. Harry Payne Bingham's *Pawnee* made very extensive collections of fishes, so many that a number of separate reports were needed to get the specimens properly studied and classified. Our interests are centered on the first report—that of Dr. Albert Eide Parr on the shallow-water bony fishes from the Bahama archipelago, and particularly on one little fish. This goby, only 22 mm. long, was taken off Crooked Island, and was "collected by Mr. Bingham from a sponge." This specimen and this statement about its habitat give us another sponge-inquiline fish. It is a new species and is named *binghami* in honor of its collector.

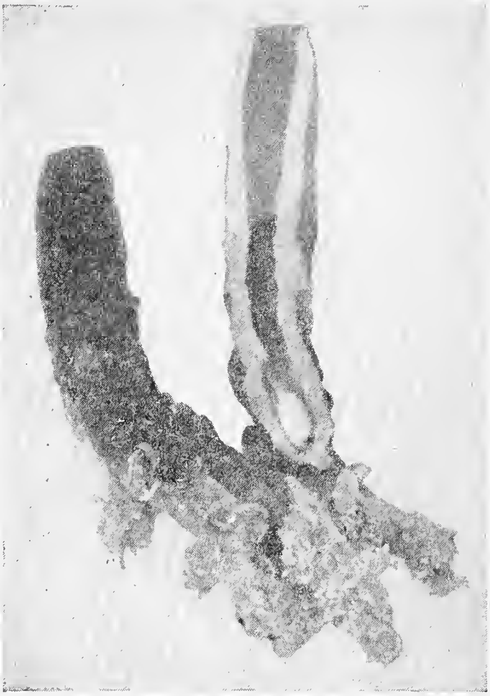
VII (1)—**Starksia cremnobates**—
Metzelaar, 1922.

Metzelaar had one specimen of this little blenny of 4 cm. "from a sponge in Curaçao Bay." The kind of sponge is not noted and Metzelaar apparently observed nothing else of the habits of the fish.

VIII (1)—**Apogonichthys puncticulatus**—
Hildebrand & Ginsburg, 1927.

My observations on the conch-dwelling habits of this fish have already been noted (Gudger, 1927). But these observations have been much extended by Hildebrand & Ginsburg (1927) who, at Key West, not only confirmed the conch-inquilinism at Marquesas, but found this fish to be a sponge-dweller also. Their statement is that—"There were found in sponges as follows: Two specimens, 37 and 40 mm. June 7, 1918; 36 mm. August 20, 1919." It would be interesting for some student at Key West to investigate this dual-inquiline habit and to see if the fish there may not have other animate lodgings—as possibly in oysters, or under the umbrella of a jellyfish. It is, so far as I know, the only fish except *Fierasfer* having a double-inquiline habit.

In 1928, Beebe & Tee-Van published their valuable work "The Fishes of Port-au-Prince Bay, Haiti." As noted above, they found a number of sponge-inquiline fishes of genera recorded earlier herein. However, they described two others to be added to the two already listed. The first is:



TEXT-FIG. 1. Longitudinal section of a finger or chimney sponge showing a little cardinal fish (*Amia pigmentarius*) in the bottom of such a sponge found in Port-au-Prince Bay, Haiti. *After Beebe*, 1928.

IX (1)—**Amia pigmentarius**—
Beebe & Tee-Van, 1928.

Of this cardinal fish taken in Port-au-Prince Bay, Beebe & Tee-Van say that their specimens without exception came from the interiors of tubular sponges and they add that in their habitat region more than fifty per cent. of the sponges examined were inhabited by these fish. See Text-fig. 1 herein —the first portrayal of this fish-sponge inquilinism. It is interesting to note that their method of collecting these Amias was by "Diving with the helmet and stuffing cotton into the different apertures of the sponges, and then sending the sponges to the surface, whence the fish were removed." Without the helmet, no specimens.

**Pomacentrus partitus** Poey, 1868.
X (1)—*Pomacentrus freemani*—
Beebe & Tee-Van, 1928.

Of this little demoiselle (48 mm. in length), our authors say "Found in a sponge which was growing on a coral reef." This is the first known record of a pomacentrid-sponge inquiline. Note, however, in the introduction to this article, a reference to an extensive symbiosis between other pomacentrid fishes and certain giant sea anemones.

In 1930, Parr, in working on the synonymy of certain forms of the genus *Pomacentrus*, found that *P. freemani* Beebe & Tee-Van is identical with Poey's *P. partitus*. So Poey's generic name of this pomacentrid takes pre-

cedence as may be seen above. This action of Parr has been followed by Longley & Hildebrand (1941). It should be noted that none of these later specimens is recorded as collected in a sponge. Hence this paragraph refers only to nomenclature. However, later on Parr and also Longley & Hildebrand will be noted as describing other little sponge-dwellers.

What Beebe & Tee-Van say of their Haitian sponge-dwellers in their systematic report on the fishes is necessarily confined to short statements of where they were collected. To get some idea of how the fishes behaved toward their sponge hosts, we must go to Beebe's interesting book, "Beneath Tropic Seas" (1928), a record of his diving around Haiti. In it Beebe writes as follows of the behavior of the sponge-dwellers. On p. 15 he speaks of three tall hollow finger-like sponges and "As I looked, a flock of small slim fish darted past and with a single turn dived into the tops of one of the [cluster of] sponges." On another occasion, while diving in order to plug such sponge openings with cotton (p. 47), he "jarred a sponge bush, whereat a tiny, lithe fish darted out . . . and popped back into the sponge." Further along (pp. 123-129) he describes how a giant black sponge ("larger than a half barrel") was located, dislocated, and finally brought to the surface and its inhabitants studied.

However, before disturbing this huge sponge, Beebe noted (p. 125) that "two fish called it home"—one a squirrel-fish which peered out from beneath the body of the sponge. The second piscine frequenter was "a pugnacious little demoiselle which had taken possession of the open center of the sponge" and only when the sponge began to be loosened up did it disappear. It would seem that the squirrel-fish was not an inquiline, but a mere wayfarer temporarily hiding beneath the sponge. At any rate, there is no hint in the systematic part of the text of inquilinism here as there is of the little demoiselle as noted above.

After the great sponge had been brought to the surface and pretty thoroughly dissected, two slender gobies less than an inch long were found (p. 126). Later three more were collected, making five (*Evermannichthys metzelaari*) in all. All these inch-long fishes were "of an even diameter which would enable them to go in and out of all but the smallest holes in the sponge surface." Evidently they were not prisoners. In all five "the united ventral fins [as noted on p. 122 herein] were extremely worn and torn . . . the tips of the rays broken and lost . . . the effects of leaving off swimming for climbing about the roughened sponge channels." One needs to read the pages noted in Beebe's book to get a full appreciation of this curious inquilinism.

This present article will now be concluded with an account of the work of Dr. C. M. Breder, Jr. (1939), who in one "hand" of tubular sponges has found three fish inquilines (each of a separate genus)—one of them a blenny, laying its eggs and hatching its young in the long sponge fingers. Surely this combination of three unlike inquiline fishes (and one of them breeding) in tubular sponges is little short of extraordinary.

Breder's studies were made in Pelican Bay near Palmetto Key, west of Useppa Island, Charlotte Harbor, Gulf coast of Florida, where abundant material was at hand. The sponges and their inquilines were in open water away from the mangroves and where there was a good tidal flow and change of water.

Under the heading "Habitat," Breder states that:

> The collection area could be waded easily at low water, and both adults and eggs [of the blenny] were taken by gathering up the very abundant yellow sponge, *Verongia fistularis* (Pallas). During the time of these collections, February, every fourth or fifth sponge would be found to contain one or more fish and a much lesser number to contain eggs, usually with an attendant parent.
>
> Associated with them in the sponge cavities were *Opsanus beta* (Goode and Bean) and *Bathygobius soporator* (Cuvier and Valenciennes). Other fishes did not seem to find these same refuges but they were shared with a large number of invertebrates.

The first of the associated inquilines to be considered is:

### XI (1)—**Bathygobius soporator**—Breder, 1939.

Breder found this goby living as an inquiline in the yellow sponges off Palmetto Key in Charlotte Harbor. Because of his preoccupation with the egg-laying blenny, he merely records this fish as a sponge inquiline. However, it is worthy of note that this is presumably the first record ever made of this habit in a fish of this genus.

The second of the inquilines is:

### XII (1)—**Opsanus beta**—Breder, 1939.

Breder found this fish also living as an inquiline in yellow sponges in shallow water. But for the reason given above, he also does not discuss the inquilinism of this fish. But this secretive habit is to be expected of a fish of this genus. At the Beaufort, N. C., Laboratory of the old U. S. Bureau of Fisheries, I found the congeneric *Opsanus tau* living and laying its eggs and guarding them in dead Venus-fan shells, in tin cans and under logs projecting under water from sand banks (see Gudger, 1910). In the light of these studies, the living of *Opsanus beta* in sponges should not be unexpected, but it is interesting that it has been found and recorded.

The third and last and most important of Breder's sponge inquilines is:

### XIII (1)—**Paraclinus marmoratus**—Breder, 1939.

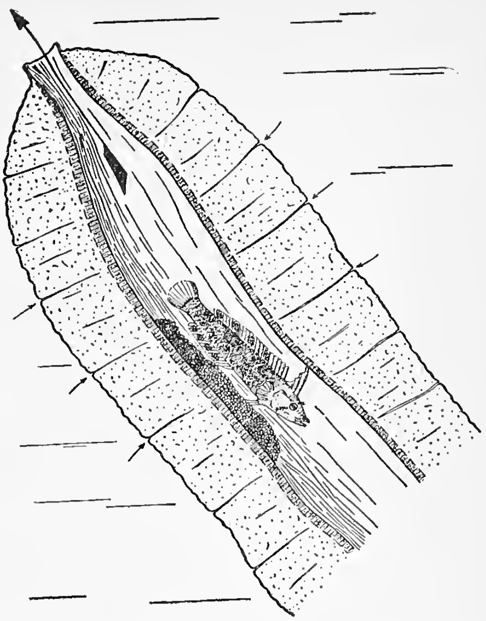
In studying the life history of this blenny,

our author has given very definite data as to its unique inquilinism. It was studied where abundant material made possible extensive observations not merely of the ordinary lodging-habit, but of its extraordinary egg-laying, hatching the eggs, and rearing its young within the tubular growths of its host. Nothing like this has ever been reported before as far as this search has revealed.

Breder's diagrammatic text-figure is reproduced as Text-fig. 2 herein. It is a sagittal section through what might be called a sponge "finger" showing the canals through which water flows in and out, as indicated by the arrows. This ensures the parent fish and the eggs a constant flow of fresh oxygen-laden water. The attendant fish is the male, and the progressive dark coloration of the eggs shows that three lots have been laid in this sponge finger.

Breder noted that "The nesting cavities selected by the fish were found to be exceedingly varied. Most frequently they were found in broken-open lumens of old sponges." These were probably of easier ingress and egress. He notes that the flow of water from the oscula of the sponges (the tip of a "finger" in Text-fig. 2 herein) is very great and hence the eggs and the guarding fish are plentifully supplied with fresh water. In many cases guardian fish were taken with the eggs. These guardians were always males —the usual sex among fishes which guard their eggs. A total of twelve nests, all in excellent condition, were carefully examined and many others in fragmentary condition were also studied.

Our narrative of this extraordinary inquilinism of three different genera of fishes, with all but the lowest of the invertebrates, fortunately ends with the nesting and breeding in the living sponge by one of the fishes —certainly a high note in animal behavior.



Text-fig. 2. Diagrammatic figure showing in vertical section the cavity of a tubular finger sponge. This serves as a nesting-place for the sponge-blenny, *Paraclinus marmoratus*, which is guarding the eggs. That the eggs are of three layings is noted by the progressive darkening coloration. The guardian fish is a male. The arrows indicate the flow of the water induced by the sponge. *After Breder*, 1939.

## Recapitulation.

Fish-sponge inquilines are recorded herein as follows: Gobies, 7 species; Blennies, 2 species; and single species of the following genera — *Amia, Apogonichthys, Opsanus, Pomacentrus*. In all, 13 species of small fishes have been recorded as living either in small finger-shaped or in big half-barrel-like sponges. All are recorded from tropical and semi-tropical waters of the central western Atlantic. Most remarkable of all is the blenny, *Paraclinus marmoratus*, which lives, lays and hatches its eggs, and brings up its young in tubular sponges.

The sponge-inquiline fishes are all small and some are noted as slender. The sponges are either tubular or finger-shaped, with terminal oscula (Text-figs. 1 and 2) into which the fishes can dive; or they are of the loggerhead vase-shaped type, in the large cavity of which the fishes can assemble or into the many lateral cavities they can worm their way to safety. The phenomenon herein considered is in all cases one-sided—the sponge gives a lodging to the fish which makes no return whatever to the sponge.

It is hoped that the publication of this article may bring to light like habits in fishes in the warm waters of the Pacific and Indian Oceans.

## Literature Cited.


Beebe, William.
1928. Beneath tropic seas: a record of diving among the coral reefs of Haiti; N. Y. (Fishes and sponges, pp. 15, 47, 125, 126-127, fig. to face p. 129).

Beebe, William & Tee-Van, John.
1928. The Fishes of Port-au-Prince Bay, Haiti. *Zoologica*, X, **1** (Fishes in sponges, pp. 120, 190, 196, 223, 224, 225).

Breder, C. M., Jr.
1939. On the life history and development of the sponge blenny, *Paraclinus marmoratus. Zoologica*, XXIV, **31** (Habitat in sponges, pp. 488-490, fig.).

Gudger, E. W.
1910. Habits and life history of the toadfish, *Opsanus tau*. Proc. 4. Internat. Fish. Cong., Washington. *Bull. U. S. Fish Comm.* (for 1908), 1910, **28**, pt. 2, 1071-1109, 7 pls.

1927. Inquilinism between the Cheilodipterid fish, *Apogonichthys puncticulatus* and the univalve mollusk, *Strombus bituberculatus. Zoologica,* IX, **2** 193-200, 1 fig.

HILDEBRAND, S. F. & GINSBURG, ISAAC.

1927. Description of new species of fishes from Key West, Fla., with notes on nine other species collected in that same locality. *Bull. U. S. Bureau Fish.* (for 1926), **42**, (p. 210, *Apogonichthys stellatus,* an inquiline in sponges and conchs).

HUBBS, CARL L.

1923. A note on the species of Evermannichthys, a genus of sponge-inhabiting gobies. *Occ. Papers Mus. Zool. Univ. Michigan,* **6**, no. 144, 2 pp.

LONGLEY, W. H. & HILDEBRAND, S. F.

1941. Systematic catalogue of the Fishes of Tortugas, Florida. *Papers Tortugas Lab. Carnegie Instit. Washington,* 34, (*Evermannichthys metzelaari* in sponges, p. 229).

METZELAAR, J.

1919. Report on the fishes collected by Dr. J. Boeke, in the Dutch West Indies, 1904-1905. In Rapport . . . de Visscherij . . . Kolonie Curaçao, etc. Tweede Gedeelte. 's-Gravenshage, (Fishes in sponges, pp. 139-140).

1922. On a collection of marine fishes from the Lesser Antilles. *Bijd. Dierk.,* Amsterdam, **22**, (Fishes in sponges, pp. 139-140).

PARR, ALBERT EIDE.

1927. Teleostean shore and shallow-water fishes from the Bahamas and Turks Island. *Bull. Bingham Oceanog. Coll.* **3**, art. 3, (*Garmannia binghami* in a sponge, p. 125).

PEARSE, A. S.

1932. Inhabitants of certain sponges at Dry Tortugas. *Papers Tortugas Lab. Carnegie Instit. Washington,* 1932, **28**, [for 1934] (*Evermannichthys metzelaari,* p. 14).

RADCLIFFE, LEWIS.

1917. Description of a new goby, *Garmannia spongicola,* from North Carolina. *Proc. U. S. Nat. Mus.,* 1917, **52**, 423-425, text fig.

# 8.

## Five New Races of Birds from Southeastern Asia.[1]

H. G. DEIGNAN.
*Associate Curator, Division of Birds, U. S. National Museum.*

The following forms, represented in the national collection of birds, have been found to require subspecific recognition. For the loan of comparative material of the woodpecker, my thanks are due the authorities of the American Museum of Natural History.

1. **Gecinulus grantia poilanei,** n. subsp.

*Type.*—U.S.N.M. no. 332424, adult [male], collected at the Arboretum of Trang Bom, Province of Bien Hoa, Cochin-China, on July 17, 1932, by A. Poilane (original number 29).

*Diagnosis.*—Nearest *G. g. indochinensis* of Tongking, but differing by having the elongated feathers of the occiput and nape brownish-buff, almost without golden suffusion (*not* olive golden), and by having the under parts deep olivaceous brown (*not* deep olive green); probably also by a slightly longer bill.

*Range.*—Cochin-China.

*Remarks.*—Inasmuch as my two specimens of *poilanei* are in somewhat worn plumage, and the feathers of woodpeckers tend to become soiled from the tree trunks, I have checked them carefully against a long series of *G. g. viridis* from Siam, the majority of which are seasonally perfectly comparable. Not even the most worn Siamese skins show any darkening of the under parts, and since *Gecinulus* is strictly confined to the non-resinous bamboos, one is probably justified in assuming that the dark coloration of the Cochin-Chinese birds has not resulted from stain.

2. **Conostoma oemodium graminicola,** n. subsp.

*Type.*—U.S.N.M. no. 314460, adult male, collected at Ndamucho ("south of Lütien [Lat. 27° 12′ N., Long. 99° 28′ E.]"), Mekong-Yangtze Divide (at elev. 14,000 ft.), northwestern Yunnan Province, China, in October, 1929, by Joseph F. C. Rock (original number 1547).

*Diagnosis.*—From both *C. oe. oemodium* of Nepal and *C. oe. bambuseti* of Szechwan, distinguished by having the color of the under parts a paler, purer ashy gray, scarcely suffused with brownish posteriorly to the throat, and by having the ashy suffusion on the head covering, not merely the front, but almost the whole crown; from *C. oe. bambuseti* further separated by its longer wing (129-139 mm., against 114-125 mm.).

*Range.*—Northwestern Yunnan.

3. **Malacopteron affine phoeniceum,** n. subsp.

*Type.*—U.S.N.M. no. 182081, adult male, collected on the Segah River, eastern Borneo, at *ca.* Lat. 2° 56′ N., Long. 117° 30′ E., on November 5, 1912, by Harry C. Raven (original number 372).

*Diagnosis.*—Strikingly different from *M. a. affine* of Malaya and Sumatra, and from *M. a. notatum* of the islands west of Sumatra, by having the pileum brownish to blackish-brown, paler anteriorly (*not* brownish-black), and the remaining upper parts *much* more strongly rufescent, with the rectrices rich ferruginous.

*Range.*—Borneo.

*Remarks.*—Chasen and Boden Kloss (*Bull. Raffles Mus.*, 4: 77, 1930), with 25 specimens before them from Bettotan and Rayoh, have written: "Absolutely inseparable from *affine* of the south of the Malay Peninsula. The crown is darkest in old birds and in a series this feature is therefore variable."

In my series of 38 skins from eastern Borneo, all adult, even the darkest-crowned individuals are readily separable from true *affine* by the characters given above.

All but three of my specimens of *phoeniceum* were taken in 1912 and 1914. Since examples of *affine* collected in 1902 and 1903 do not differ appreciably from others shot in 1926, it may be assumed that the strong rufescence of the Bornean material is not attributable to post-mortem change of color.

Skins from western Borneo somewhat approach *affine,* but are nevertheless nearer *phoeniceum,* especially in the color of the tail.

4. **Geokichla citrina gibson-hilli,** n. subsp.

*Type.*—U.S.N.M. no. 178809, adult male, collected at Sungei Balik (*ca.* Lat. 10° 31′ N., Long. 98° 33′ E.), Mergui District, Tenasserim Division, Burma, on November 29, 1900, by William L. Abbott.

*Diagnosis.*—From *G. c. citrina* of India distinguished by its longer and heavier bill and by having the orange rufous portions of the plumage richer and brighter; from *G. c. rubecula* of Java, by having both the orange rufous and the slaty blue parts of the plum-

[1] Published by permission of the Secretary of the Smithsonian Institution.

age decidedly paler; from *G. c. innotata* of Siam and Indo-China, by having the median upper wing coverts conspicuously tipped with white.

*Range.*—Central third of the Malay Peninsula.

*Remarks.* — This form, known only by winter-taken specimens, is probably resident from southern Tenasserim to the Siamese Province of Trang.

5. ***Anthreptes singalensis stellae,*** n. subsp.

*Type.*—U.S.N.M. no. 311273, adult male, collected on Khao Saming (Lat. 12° 21′ N., Long. 102° 27′ E.), Trat Province, southeastern Siam, on October 16, 1928, by Hugh McC. Smith (original number 2510).

*Diagnosis.*—Nearest *A. s. koratensis* of eastern Siam, with which it agrees in having the color of the throat and upper breast sharply divided from that of the remaining under parts, but separable therefrom, sex for sex, by having the chestnut rufous of the anterior under parts decidedly deeper, and the color of the lower breast and belly more purely golden, less greenish, yellow.

*Range.*—Southeastern Siam.

# 9.

# A Survey of *Pasteurella tularensis* Infection in the Animals of the Jackson Hole Area.[1]

Mitsuru Nakamura.
*Department of Bacteriology, University of Southern California.*

## Introduction.

In a wooded wildlife area such as Jackson Hole, Wyoming, there are possibilities of the infection of human beings by tularemia, a bacterial infection caused by *Pasteurella tularensis*. It is prevalent in the Rocky Mountain and Pacific Coast regions and is especially associated with the abundance of ticks and deerflies in these areas. Since this infection is directly transmissible to man through contact with infected animals as well as through the bite of an arthropod harboring the organism, a survey to determine the prevalence of tularemia in this area was considered important. Although tularemia may be transmitted through the bites of the wood tick (*Dermacentor andersoni*), the American dog tick (*Dermacentor variabilis*), the lonestar tick (*Amblyomma americanum*), the Pacific Coast tick (*Dermacentor occidentalis*), the deer tick (*Ixodes pacificus*) and deer flies, for our purposes in the Jackson Hole area the Rocky Mountain wood tick (*D. andersoni*) is probably the only intermediate host of importance.

Tularemia is known to occur in rabbits, particularly jack rabbits, and in other rodents. Kohls and Steinhaus (1943) have reported it in the shrew, *Sorex vagrans monticola*, and the field mouse, *Microtus pennsylvanicus modestus*. Tularemia has been found in sheep by Parker and Dade (1929). Epizoötic tularemia in sheep in Montana was due entirely to the wood tick according to Philip, Jellison and Wilkins (1935). Although wild rabbits and hares have caused more than 90 per cent. of all the human cases reported in the United States, other rodents have been found to harbor the disease-producing organisms (Jellison and Parker, 1944). Jellison and his co-workers (1942) have reported epizoötic tularemia in the beaver, *Castor canadensis*. Tularemia has been contracted by human beings from the ground squirrel, tree squirrel, woodchuck, cat, dog, hog, fox, coyote, muskrat, deer, mink, raccoon, grouse and pheasant (Foshay, 1946).

The ticks may infect man not only by their bite, but also by their excrement (Parker, 1935). Davis (1943) attempted to transmit *P. tularensis* to man through the bedbug (*Cimex lectularius*), but concluded that this mode of transmission was unreliable. The same author (Davis, 1940) reported that the organisms may survive in the argasid ticks (*Ornithodoros turicata* and *O. parkeri*) for at least 674 and 701 days, respectively, but that they did not transmit the organisms during feeding.

This paper is a report of a general tularemia survey made during the summer of 1949 of the rodents and other animals in the Jackson Hole area. The results of examinations of ticks collected in this area are included. The first phase only of the tularemia problem in Jackson Hole is reported on, namely: a determination of the occurrence of tularemia in rodents and other wild animals found in this area. No studies have been made of the epidemiology.

## Materials and Methods.

Various mammals were collected in the Jackson Hole area during the period of June 2 to August 20, 1949. Live traps were used where possible, but shooting and other methods of hunting were also used. In order to make a general survey, the trapping was not restricted to single species. Protected animals such as the beaver and mink were not taken unless found dead.

Upon capture of an animal, blood was drawn from the heart and a Gram stain made from a smear. The blood was also used to inoculate a blood-glucose-cystein (Difco) slant. The tubes were incubated at 37° C. for 3 to 5 days. Periodic examinations were made of the slant cultures. None of the tubes was discarded as negative until incubated two weeks. When growth occurred on the slants, Gram stains were again made to compare with the organisms originally seen in the blood.

The animal was dissected after the blood was drawn and a careful examination made of the liver, kidney and spleen to detect characteristic lesions. When these organs

[1] Contribution of the 1949 Summer Research Program at the Jackson Hole Biological Station of the New York Zoological Society.

Acknowledgments: The author is greatly indebted to Mr. James R. Simon, Director of the Jackson Hole Wildlife Park, for his generous suggestions. Appreciation is due Mr. James S. Findley, Western Reserve University, Ohio, and Mr. Norman C. Negus, Miami University, Ohio, for aid in collecting and identifying some of the mammals.

were abnormal, tissue from them was used to inoculate a blood-glucose-cystein slant and incubated for 3 to 5 days and the subsequent growth was examined after Gram staining to detect typical Gram-negative, encapsulated, pleomorphic rods.

A physiological saline solution suspension was made if tularemia-like organisms were isolated from the growth and 1 cc. of this suspension was injected intraperitoneally into a laboratory mouse. After 7 to 9 days, it died if the injected organisms were *P. tularensis*. The mouse was then autopsied and its blood used to inoculate a blood-glucose-cystein slant. If tularemia organisms were detected, the specimen was considered positive for tularemia.

The method described by Philip, Jellison and Wilkins (1935) was used in the examination of the wood ticks. Adult, unfed ticks were swept from the vegetation in the area by "flagging." The ticks thus collected gave a fairly accurate quantitative estimate of active tick populations. After a certain area or field was "flagged," the ticks collected were placed separately in glass vials, macerated with a sterile glass rod and normal physiological saline solution was added to make a uniform suspension of the organisms. The vial was corked and shaken 15 times. From this suspension a Gram stained preparation was made and examined microscopically under the oil-immersion lens. A loopful of this suspension was transferred to a blood-glucose-cystein slant and incubated for 3 to 5 days at 37° C. After the incubation period, if growth had occurred, Gram stains were made from the slants. These slides were also examined under the oil-immersion lens.

## Results.

A total of 152 mammals of 15 species and 56 ticks were examined. The number examined and the number of positives are given in Table I.

TABLE I.

| *Mammal* | *No. examined* | *No. positive* |
|---|---|---|
| Red-backed mouse (*Clethrionomys gapperi idahoensis*) | 8 | 0 |
| Jumping mouse (*Zapus princeps*) | 13 | 2 |
| White-footed deer mouse (*Peromyscus maniculatus artemisiae*) | 22 | 2 |
| Long-tailed weasel (*Mustela frenata nevadensis*) | 8 | 0 |
| Uinta ground squirrel (*Citellus armatus*) | 23 | 4 |
| White-tailed jack rabbit (*Lepus townsendii campanius*) | 6 | 1 |
| Uinta chipmunk (*Eutamias umbrinus*) | 11 | 0 |
| Wind River pine squirrel (*Tamiasciurus hudsonicus ventorum*) | 31 | 3 |
| Pocket gopher (*Thomomys talpoides tenellus*) | 1 | 0 |
| Buff-bellied chipmunk (*Eutamias amoenus luteiventris*) | 10 | 0 |
| Least chipmunk (*Eutamias minimus*) | 11 | 2 |
| Mink (*Mustela vison*) | 1 | 1 |
| Badger (*Taxidea taxus taxus*) | 2 | 1 |
| Porcupine (*Erethizon dorsatum epizanthum*) | 4 | 1 |
| Flying squirrel (*Glaucomys sabrinus*) | 1 | 0 |

Of the 152 animals examined, there were 17 positives for tularemia, which was detected in the jumping mouse, white-footed deer mouse, Uinta ground squirel, white-tailed jack rabbit, Wind River pine squirrel, least chipmunk, mink, badger and porcupine. This is believed to be the first report of tularemia in the badger (*T. t. taxus*) and the porcupine (*E. d. epizanthum*).

Only one of the 56 ticks examined gave a positive reaction for *P. tularensis*.

## Discussion.

At this time a percentage estimate of the occurrence of tularemia in the Jackson Hole region cannot be given accurately, the number of animals collected not being large enough to warrant conclusions on this point. In six species tularemia was not detected, but conclusive evidence that these species living in the Jackson Hole area do not contract tularemia is lacking. Further work in this respect is definitely necessary.

Correlation of the number of infected ticks and the number of animals with tularemia could not be established, since only one out of the 56 ticks was found to be infected.

Many of the animals diagnosed as positive for tularemia did not have enlarged spleens or focal necrosis. They were not sluggish or sick-looking, probably because they were caught while in the early stage of the infection.

According to Jellison (1949), who worked in Teton County where the Jackson Hole region is situated, tularemia should be expected to be rare, because there are no cottontail rabbits. There are, however, a number of jack rabbits and snowshoe hares, although considerably fewer than in similar areas.

Mammalogists at the Jackson Hole Wildlife Park Research Center handled and skinned during the summer a certain number of small mammals that were later detected as having had tularemia. Exposure to the disease through this work did not lead to infection, perhaps because of the low virulence of some of the *P. tularensis* strains found in resident rodents. The organisms in these rodents are the least virulent; those

found in sheep are the most virulent (Jellison, 1949).

## Conclusions.

1. Tularemia may occur in the badger and the porcupine.

2. Tularemia is found in some of the rodents and other small mammals of the Jackson Hole region.

3. Tularemia has been detected in the jumping mouse, white-footed deer mouse, Uinto ground squirrel, white-tailed jack rabbit, Wind River pine squirrel, least chipmunk, mink, badger, and porcupine in the Jackson Hole region.

4. The incidence of tularemia in Teton County, Wyoming, seems to be relatively low due to the region's isolation and small rabbit population.

5. The virulence of *P. tularensis* found in rodents of this region is low and is not very likely to cause cases of human tularemia.

## Bibliography.


Davis, G. E.

1940. *Bacterium tularense*: Its persistence in the tissues of the Argasid ticks *Ornithodoros turicata* and *O. parkeri*. *Pub. Health Repts.*, 55: 676-680.

1943. Further attempts to transmit *Pasteurella tularensis* by the bedbug (*Cimex lectularius*). *Jour. Parasit.*, 29: 395-396.

Jellison, W. L., G. M. Kohls, W. J. Butler and J. A. Weaver.

1942. Epizoötic tularemia in the beaver, *Castor canadensis* and the contamination of stream water with *Pasteurella tularensis*. *Am. Jour. Hyg.*, 36: 168-182.

Jellison, W. L. and R. R. Parker.

1944. Rodents, rabbits and tularemia in North America: Some zoological and epidemiological considerations. *Am. Jour. Trop. Med.*, 25: 349-362.

Jellison, W. L.

1949a. Personal communications.

1949b. Paper read at the International Northwestern conference on Diseases of Nature Communicable to Man, Aug. 24, 25, and 26, 1949.

Kohls, G. M. and E. A. Steinhaus.

1943. Tularemia: Spontaneous occurrence in shrews. *Pub. Health Repts.*, 58: 842.

Parker, R. R.

1935. Tick-caused tularemia in man. Rocky Mountain Laboratory Station Circular No. 3, First Revision, March, 1935.

Parker, R. R. and J. S. Dade.

1929. Tularemia in sheep in nature. *Pub. Health Repts.*, 44: 126-130.

Philip, C. B., W. L. Jellison and H. F. Wilkins.

1935. Epizoötic tick-borne tularemia in sheep in Montana. *J. Am. Vet. Med. Assoc.*, 86: 726-744.

# 10.

# Neotropical Chilopods and Diplopods in the Collections of the Department of Tropical Research, New York Zoological Society.[1]

RALPH V. CHAMBERLIN.
*University of Utah, Salt Lake City.*

(Text-figures 1-23).

The present paper is a report upon a collection of tropical chilopods and diplopods submitted to me for study through the courtesy of Dr. William Beebe. The material was secured in the course of several expeditions directed by Dr. Beebe and carried out under the auspices of the Department of Tropical Research of the New York Zoological Society.

As shown by the following list of species taken at the several localities represented, the greater part of the material was collected in British Guiana, and more especially in Venezuela, during the years 1945 and 1946. It makes possible a considerable addition to our knowledge of the myriopod fauna of northern South America. That much remains to be done, however, is plainly indicated by the large percentage of new forms represented in the collection here surveyed.

Four new genera and 23 new species are described. All types and the entire collection are deposited in the American Museum of Natural History, New York City.

## CONTENTS.[2]



## Class Chilopoda.
## Order Scolopendrida.

### CRYPTOPIDAE.

#### *Newportia diagramma* Chamberlin.

*Newportia diagramma* Chamberlin, 1921, *Occ. Papers Univ. Mich.*, 4(97) ; *2: 8, 9.

Locality: British Guiana: Kartabo. (T.R. S. 3058). One specimen.

Described originally from British Guiana at Dunoon, Labba Creek.

#### *Newportia monticola* Pocock.

*Newportia monticola* Pocock, 1890, *Ann. Nat. Hist.*, ser. 6, 6:144.

*Newportia rogersi* Pocock, 1896, Biol. Centr. Amer. Chilopoda, p. 34, *3:6.

---

[1] Contribution No. 878, Department of Tropical Research, New York Zoological Society.

[2] This Table of Contents is organized according to the origin of specimens, rather than on a systematic basis.

Locality: Venezuela: Rancho Grande. One specimen taken in July-August, 1946, on the jungle floor.

This species was previously known from Ecuador, Colombia and Costa Rica.

**Newportia phoretha,** new species.

Head and basal plate dark chestnut, the other tergites a lighter chestnut or brown.

Antennae composed of 7 articles of which the first three bear chiefly longer setae, the others almost exclusively shorter and finer, more dense hairs. Edge of prosternum gently convex on each side, obtusely excavated at middle.

Head without sulci. First dorsal plate with a sharply impressed, semi-circular sulcus but with no distinguishable paired sulci. Paired complete on second and subsequent tergites. Tergites showing in addition a coarser, deeper sulcus on each side toward the lateral border. Some plates show also a median furrow but no true keel.

Sternites with no paired sulci but with a strong median furrow over the posterior two-thirds or more of length.

Tibia of anterior legs with neither lateral nor ventral spine although occasionally a mid-ventral hair is more than usually strengthened in a way suggestive of a nascent spine. Tibiae with the usual spine at distal end above.

Prefemur of anal legs in the type with 4 large ventral spines; the femur with 2 spinules on mesal side; tarsus with 8 distinct joints on one leg and 10 on the other, with distal end of the latter lost.

Length: 35 mm.

Locality: Venezuela: Rancho Grande. Three specimens in bromeliads in June, July and August of 1945 and 1946.

One specimen referred to this species as a paratype has 11 segments to each tarsus of the anal legs. It differs in showing vague traces of paired sulci on the first tergite.

This species seems to be closest to *N. pusilla* Pocock but differs from it as well as from other known species in lacking both ventral and lateral tibial spines on the anterior legs.

Material: Holotype No. 461208, Paratype No. 461209.

**Otocryptops ferrugineus** (Linnaeus).

*Scolopendra ferruginea* Linnaeus, 1767, Syst. nat., 12:1063.

*Otocryptops ferrugineus* Pocock, 1893, *Jour. Linn. Soc. London,* 24:463.

Localities: Venezuela: Rancho Grande. Six specimens taken in June, July and August, 1946. Caripito: One specimen taken in July.

This species has been recorded from many localities in America from Mexico south to Brazil and Ecuador, and in Africa from the western portion.

**Otocryptops melanostomus** (Newport).

*Scolopocryptops melanostomus* Newport, 1845, *Trans. Linn. Soc. London,* 19:406.

*Otocryptops longiceps* Haase, 1887, *Abh. Mus. Dresden,* No. 5:98; *6:106.

*Otocryptops melanostomus* Pocock, 1893, *Jour. Linn. Soc. London,* 24:464.

Localities: Venezuela: Rancho Grande. Two specimens taken in bromeliads in July and August. Cocos Is.: One specimen taken on *Arcturus* Expedition, May 22, 1925.

Previously recorded from many localities in the East Indies and in the western hemisphere from Central America south to Argentina.

OTOSTIGMIDAE.

**Otostigmus beebei,** new species.

General color olive, with the legs light brown.

Antennae composed of 17 segments of which the first 2½ are glabrous. Head sparsely punctate. Prosternal teeth 4+4.

Dorsal plates from the third on with complete and fine paired sulci. Only the last tergite truly margined. The last few tergites finely scabrous, the prickles more or less in longitudinal lines; the other plates essentially smooth.

Sternites smooth and without pits or furrows except a median pit on the sternites of the middle region. Last sternite narrowing caudad; its caudal margin weakly incurved.

Coxopleural process short, rounded distally and unarmed.

Last legs wholly unarmed, smooth throughout. Last two pairs of legs without tarsal spines; all others with a single tarsal spine.

Length: 70 mm.

Localities: Venezuela: Rancho Grande. Three specimens were taken on the jungle floor in May and June, 1946, and two on July 25, 1948, by Dr. Beebe.

Structurally this species would seem to be related to *O. goeldi*, but it is a much larger form, the length of the latter species being only about 24 mm. It differs also, e.g., in having but a single tarsal spine on all the anterior legs.

Material: Holotype No. 461215, Paratype No. 461216.

**Otostigmus caducus,** new species.

Head and first three tergites chestnut colored, the rest of the dorsum olive green. Antennae with first two segments olive, the others brown and distally becoming brown. Legs olive green.

Head smooth. Antennae composed of 18 articles of which none is completely glabrous.

Prosternal teeth 4—4, the two middle ones on each side more widely separated from each other than from those at ends of series; the dental plate wider than long.

Only the tergites from the 12th on sulcate, the sulci where present complete. Tergites of posterior region typically with six longitudinal ridges, sparsely scabrous keels and the outer borders of tergites more or less rugose. A median keel developed only on the more posterior tergites, where present not

high. Only the 21st tergite sharply margined, but others with margin set off by a shallow depression, being what might be called pseudo-margined. Last tergite with a median furrow on posterior portion.

Sternites without definite furrows or pits.

Coxopleurae produced slightly in a rounded prominence on inner side, the posterior margin bearing no spines. Poriferous area reaching caudal margin.

Prefemur of anal legs entirely unarmed. Only the first pair of legs with two tarsal spines.

Length: 38 mm.

Localities: Venezuela: Rancho Grande.

Apparently most nearly related to *O. scabricauda* (H. and S.) and *O. rex* Chamberlin, known from Colombia and Brazil.

Material: Holotype No. 45462.

**Otostigmus pococki** Kraepelin.

*Otostigmus pococki* Kraepelin, 1903, *Int. Mus. Hamburg*, 20:124; *62, 63.

Locality: British Guiana: Kartabo. Six specimens.

SCOLOPENDRIDAE.

**Scolopendra alternans** Leach.

*Scolopendra alternans* Leach, 1815, *Trans. Linn. Soc. London*, 11:383.

Locality: West Indies: Santa Lucia. Two specimens taken July 12, 1932.

This characteristically West Indian species occurs also in Florida, Venezuela and Brazil.

**Scolopendra galapagoensis** Bollman.

*Scolopendra galapagoensis* Bollman, 1890, *Proc. U. S. Nat. Mus.*, 12:215.

Locality: Hood Island, Galapagos. Three small specimens were taken May 27, 1925.

**Scolopendra subspinipes** Leach.

*Scolopendra subspinipes* Leach, 1815, *Trans. Linn. Soc. London*, 11:383.

Localities: British Guiana: Kartabo. Three specimens. Bermudas: two specimens taken Aug. 24, 1929.

**Scolopendra viridicornis** Newport.

*Scolopendra viridicornis - punctidens - variegata-cristata* Newport, 1844, *Ann. Nat. Hist.*, 13:97, 98.

Locality: British Guiana: Kartabo. Three specimens.

## Order Geophilida.

SCHENDYLIDAE.

**Nesondyla**, new genus.

A genus in most features resembling the palearctic *Brachyschendyla* but differing in having the margins of the claw of the second maxillae closely pectinate. Teeth of mandible in one block; long and slender. Labrum widely concave or incurved and bearing numerous strongly developed teeth. In middle of clypeal region a more finely areolate spot bearing two setae. Ventral pores lacking on sternites. Coxopleural pores two on each side, these large and homogeneous. Last ventral plate wide. Telopodite of anal legs six-jointed, the tarsus consisting of two articles and clawless.

Orthotype: *Nesondyla nealota*, new species.

**Nesondyla nealota**, new species.

Head a little longer than wide; anterior margin gently convex from side to side, the caudal margin a little incurved and the lateral margins convex throughout. Frontal suture not present, antennae unusually long.

Prebasal plate exposed. Claws of prehensors when closed nearly even with anterior margin of head. All joints unarmed. Chitinous lines not present.

Last ventral plate broad, the posterior corners rounded and the caudal margin gently convex. Coxal pits large, two on each side of which the posterior one is free and the anterior one partly covered.

Pairs of legs: 51.

Length: about 29 mm.

Locality: Hood Island. One specimen taken Apr. 27, 1925.

Material: Holotype No. 2567.

BALLOPHILIDAE.

**Cerethmus naiquatanus** Chamberlin.

*Cerethmus naiquatanus* Chamberlin, 1941, *Proc. Biol. Soc. Wash.*, 54:140.

Locality: Venezuela: Rancho Grande. One male taken in May-June, 1946, by Dr. Beebe.

The type locality of this species is also Venezuela at Los Canales, Naiquata. The specimen here recorded from Rancho Grande is larger than the holotype, its length being 62 mm. as against 40 mm. It has 85 pairs of legs while the holotype has 81. The peculiar antennae are as in the holotype but with less indication of geniculation at the middle. The labrum presents a well-sclerotized edge on each side but not at the middle where there is a soft protruding swelling; no teeth or pectinae. First maxillae with a lappet from each outer angle of the coxite but the telopodite lacking a lappet. Claws of palpi of second maxillae closely pectinate. Anal legs strongly crassate.

ORYIDAE.

**Notiphilides maximiliani miranda** (Chamberlin).

*Keporya miranda* Chamberlin, 1941, *Proc. Biol. Soc. Wash.*, 54:139.

Type Locality: Venezuela: Miranda: Curupas, Los Canales.

New Locality: Venezuela: Rancho Grande. Two adult females and a partly grown specimen were taken in May-June, 1946, by Dr. Beebe.

This form is maintained apart from *maximiliani*, sens. str., on the basis of a more distinct indication of a frontal suture by a fine furrow along a pale line. This, however, varies in distinctness and may not prove a dependable character for separation of the two forms. In the one female dissected the mandible shows only four pectinate lamellae

instead of the six given by Attems as typical for the true *maximiliani*. The basal plate in typical *maximiliani* seems normally to be about as long as the succeeding tergite, whereas in the Venezuelan form it is only about half as long or but little more, as is also recorded by Brolemann for his *N. grandis*. Of the two adult females from Rancho Grande, one has 87 pairs of legs, the other 95 pairs.

**Orphnaeus brevilabiatus** (Newport).

*Geophilus brevilabiatus* Newport, 1845, *Trans. Linn. Soc. London*, 19:436.

*Orphnaeus lividus* Meinert, 1870, *Naturh. Tidsskr.*, ser. 3. 7:19.

*Orphnaeus brevilabiatus* Haase, 1887, *Abh. Mus. Dresden*, nr. 5: 111; *117.

Locality: Hood Id., Galapagos. One specimen taken May 27, 1925.

This is one of the most abundant and widespread of geophilid chilopods, occurring in all tropical areas of America, India and Africa and the Pacific islands.

## Order Scutigerida.

### SCUTIGERIDAE.

**Pselliodes colombiana** Chamberlin.

*Pselliodes colombiana* Chamberlin, 1921, *Occ. Papers Mus. Zool. Mich.*, 97:25.

Locality: Venezuela: Rancho Grande. Five specimens of various sizes, two of them exceptionally large. A small specimen was taken in a bromeliad on June 6, 1946.

# Class Diplopoda.

## Order Glomeridesmida.

### GLOMERIDESMIDAE.

**Glomeridesmus obvius,** new species.

A somewhat smaller species than the Colombian *G. porcellus* Gervaia and Goudot, as identified and redescribed by Brolemann, the width being 2.5 mm. as against 3 mm., while broader than the *G. trinidadensis* of Loomis, the width of which is given as 2 mm. The length of the type of the present species is close to 11 mm.

It differs conspicuously in color pattern from the other two species mentioned. The head is dusky chestnut or reddish in front, but yellow on the sides; there are two dark spots between the antennae. Antennae dusky over yellow. The dorsum behind the collum shows a wide longitudinal band of black color enclosing three longitudinal series of yellow spots; the sides yellow except for a series of black marks, each mark in the form of an angular stripe about the anterior corner of the keel, one arm extending mesad along the anterior margin, the other back to middle along the lateral border. Venter and legs yellow.

Lateral keels with posterior corners rounded, being acutely produced only on the 18th and 19th segments.

Locality: Venezuela: Rancho Grande. One specimen taken in May-June, 1946.

Material: Holotype No. 461210.

## Order Cambalida.

### CAMBALIDAE.

**Phanolene,** new genus.

Body of the form usual in the family. Eyes present, forming a single series paralleling the margin of the collum. Antennae moderately stout, clavate.

Collum overlapping posterior border of head; about as long as the two following tergites together; wholly smooth.

Body obviously constricted behind the collum. Keels of second segment only weakly developed, better developed on the third and of normal size on the fourth. Pores beginning on fourth. Tergites with five strongly developed keels between the porigerous keels. Anal tergite smooth; not projecting beyond the anal valves.

Orthotype: *Phanolene sima*, new species.

Differing from *Cambala* in having five crests between the porigerous keels and in having claws on the first legs.

**Phanolene sima,** new species.

Text-figs. 1 & 2.

Ocelli four on each side. A sharp keel or ridge below outer edge, leaving below it a furrow into which the antenna fits. Antennae widely separated; 5th and 6th joints much swollen, making the antennae strongly clavate.

Collum entirely smooth. Second and especially the third and fourth segments narrower, producing a neck-like constriction. Second segment with crests distinct but short, these becoming longer on third and fourth segments. The pore borne at anterior end of its keel, the porigerous swelling nearly circular in outline. Below the porigerous keel six to eight crests which decrease in height and distinctness ventrad.

Anterior pairs of legs without any special processes or lobes.

Gonopods of male as shown in Text-figs. 1 and 2.

Number of segments: 58.

Length: about 21 mm.; width, 1 mm.

Locality: British Guiana: Kartabo. One male taken April 15.

Material: Holotype No. 241050.

## Order Spirobolida.

### RHINOCRICIDAE.

**Neocricus encantus** Chamberlin.

*Neocricus encantus* Chamberlin, 1941, *Bull. Univ. Utah, Biol ser.*, 6(4):15.

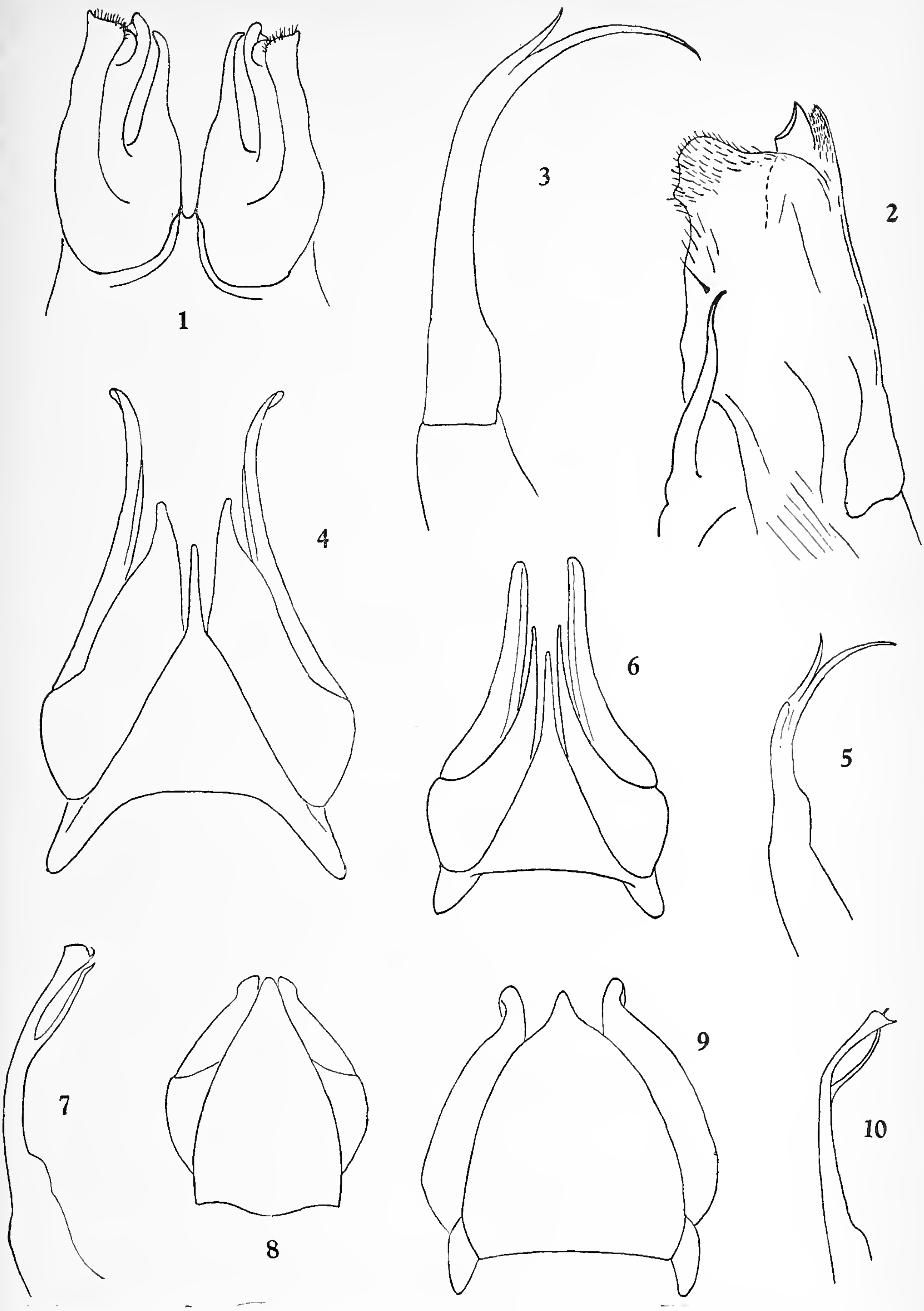
Locality: Venezuela: Caripito. One female taken in July. Rancho Grande: A male taken May 26, 1948.

The type of this species was taken in Venezuela at El Cantado, which is near Petare in Miranda, by G. Vivas-Berthier.

**Neocricus permundus,** new species.

Text-figs. 3 & 4.

A larger and darker form than *N. foederatus* Chamberlin. General color of body




TEXT-FIG. 1. *Phanolene sima* n. sp. Anterior gonopods, cephalic aspect. TEXT-FIG. 2. *Phanolene sima* n. sp. Posterior gonopod. TEXT-FIG. 3. *Neocricus permundus* n. sp. Posterior gonopod. TEXT-FIG. 4. *Neocricus permundus* n. sp. Anterior gonopods, cephalic aspect. TEXT-FIG. 5. *Neocricus tivior* n. sp. Posterior gonopod. TEXT-FIG. 6. *Neocricus tivior* n. sp. Anterior gonopods. TEXT-FIG. 7. *Rhinocricus monilicornis* (Porat). Posterior gonopod. TEXT-FIG. 8. *Rhinocricus monilicornis* (Porat). Anterior gonopods. TEXT-FIG. 9. *Rhinocricus acrotypus* n. sp. Anterior gonopods. TEXT-FIG. 10. *Rhinocricus acrotypus* n. sp. Posterior gonopod.

typically black with caudal borders of metazonites dark chestnut or dark Indian red. Legs dark red.

Head smooth. Median sulcus fine, distinct across vertex and on lower part of face. Eyes separated by nearly three times their longer diameter. Clypeal foveolae 2—2.

Collum without distinct sulci except the anterior margining one on each side below level of eye.

Repugnatorial pores normally beginning on the sixth segment; sometimes missing from the seventh segment on one or both sides; pores in contact with sulcus on its anterior side. Segmental sulci distinctly impressed throughout, only a little curved at level of pore. Metazonites longitudinally striate below as usual and essentially smooth above. Prozonites with finer, more oblique, partly anastomosing striae below, these becoming transverse above. Scobina of middle segments consisting of a rather weak lunate impression on border followed by a narrowly triangular area composed of fine striae, the sides of this striate area concave, the narrow terminal part typically prolonged; scobina beginning at the eighth or ninth segment and continuing to the 38th; on the more anterior segments the lunate impression may be absent or but weakly indicated.

Last tergite with cauda much exceeding the valves; gently curving upward at tip.

The gonopods of the male are as shown in Text-figs. 3 and 4. The sternite, as in other species of the genus, much prolonged apically; exceeded by the prolonged coxal pieces of the anterior gonopods. Branches of the posterior gonopods very unequal.

Number of segments: 44.

Length of male holotype: nearly 140 mm.; diameter, 9.3 mm. Diameter of female allotype: 12 mm.

Locality: Venezuela: Rancho Grande. Among "shrubs and trunks" on jungle floor. Several specimens collected by Dr. Beebe.

This species is close to *N. caudatus* (Brolemann), but differing in its much darker coloration and apparently in details of the gonopods, such as in the more slender, better set-off, apical portion of the sternite and the longer, more slender telopodites of the anterior pair.

Material: Holotype No. 461223, Allotype No. 461224, Paratypes No. 461225, No. 461226, No. 461227, No. 461228, No. 461229.

**Neocricus tivior,** new species.

Text-figs. 5 & 6.

A considerably smaller form than *N. foederatus* and lacking the strongly contrasting color annuli of the latter, the color being a dull chestnut or reddish-brown, with annuli on caudal borders of metazonites often not well defined. Legs ferruginous.

Head smooth; median sulcus fine across vertex and down lower part of face but obscure or absent at level of antennae as usual. Collum without sulci other than the usual margining one.

Segmental sulcus distinct throughout. Pores beginning on the sixth segment, each in contact with the sulcus which is gently excurved at its level. The usual anastomosing striae on prozonite and similar markings also present on dorsum behind the sulcus. Longitudinal sulci below on metazonites fine. Scobina consisting of a deep lunate impression followed by the usual series of striae; separated by nearly three times the transverse width of the lunate impression; beginning on seventh segment and present back to the fifth or sixth from the last segment.

The coxal division of the anterior gonopods distally very slender, distinctly but not greatly exceeding the slender distal tongue of the sternite; telopodite slender and distally straight as shown in Text-fig. 6. In contrast to that of *chacaitus* the anterior branch of the posterior gonopods is larger, curving and divergent as shown in Text-fig. 5.

Number of segments: 45.

Locality: Venezuela: banks of the Ocumare river. Male holotype taken April 23, 1946.

Aside from its much smaller size, this form differs superficially from *N. foederatus*, to which seemingly it is most closely allied, in having the characteristic anastomosing fine striae of the tergites much less strongly developed, with the lines more broken on the metazonites dorsally than in *foederatus* in which they are densely and strongly developed over the entire metazonite. The lunate impression of the scobina deeper and more uniformly developed than in *foederatus*.

Material: Holotype No. 461222.

**Neocricus conclusus,** new species.

Text-figs. 22 & 23.

Very close to *N. encantus* Chamberlin in color pattern and in structure, but a considerably smaller form in which the characteristic sculpturing of the metazonites is less strongly developed.

The sternite of the anterior gonopods has the distal tongue shorter, much more exceeded by the coxae than *encantus*. The posterior gonopods have the two distal branches more nearly equal in length and less divergent, with the outer branch but little curved. See further Text-figs. 22 and 23.

Number of segments: 43.

Width: 5.6 mm.

Locality: Venezuela: Rancho Grande. Male holotype taken during May-June, 1946, by Dr. Beebe.

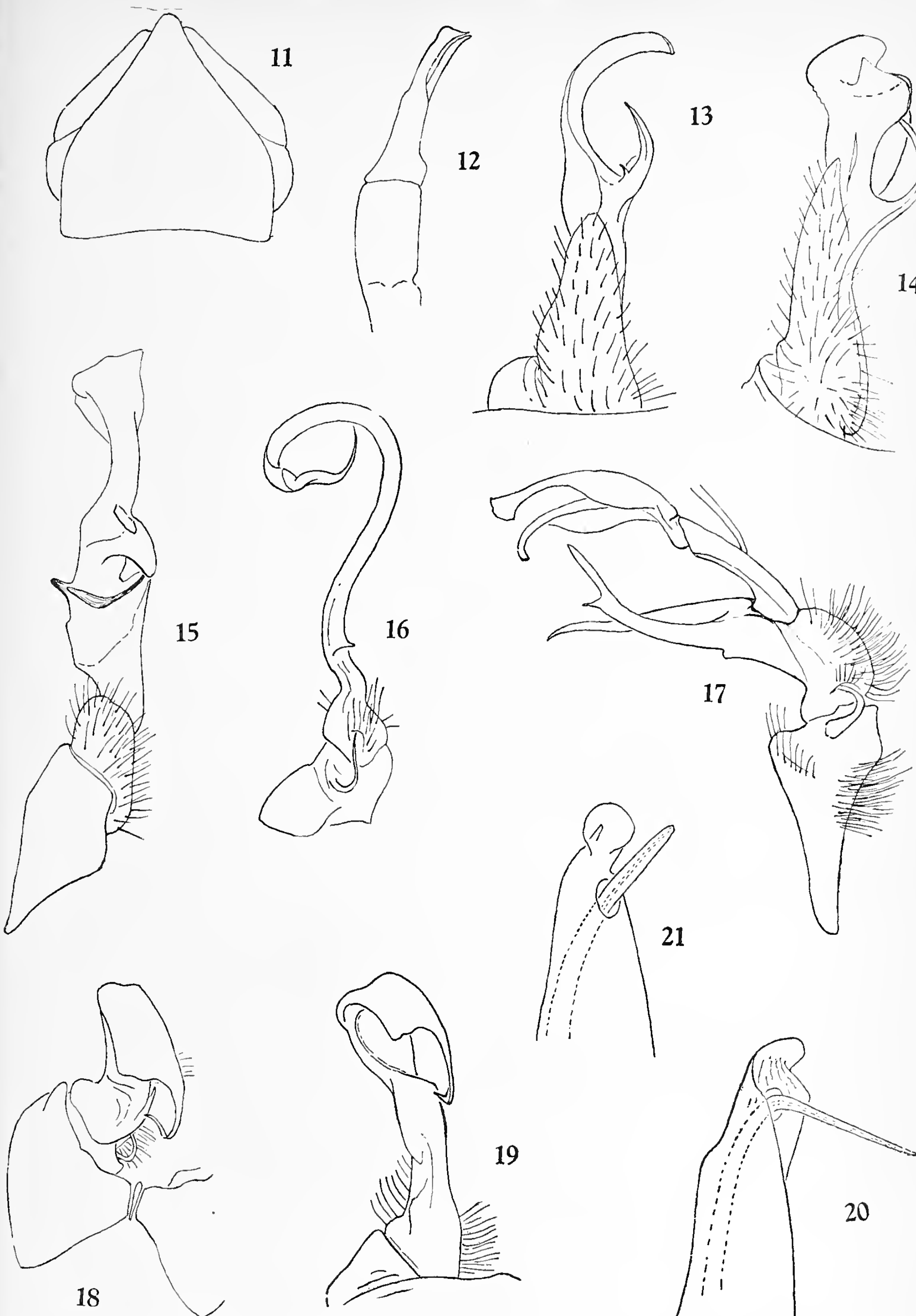
Material: Holotype No. 461207.

**Neocricus ruberculinus** (Silvestri)

*Rhinocricus ruberculinus* Silvestri, 1898, *Anal. Mus. Nac. Buenos Aires*, 6:77.

Type Locality: Venezuela: Caracas. Female holotype taken by Mienert and preserved in the Copenhagen Museum.

New record: Venezuela: Rancho Grande.




Text-fig. 11. *Rhinocricus finitis* n. sp. Anterior gonopods. Text-fig. 12. *Rhinocricus finitis* n. sp. Posterior gonopod. Text-fig. 13. *Amplinus beebei* n. sp. Left gonopod in situ, caudal aspect. Text-fig. 14. *Aphelidesmus confluens* n. sp. Gonopod. Text-fig. 15. *Aphelidesmus frangens* n. sp. Gonopod. Text-fig. 16. *Ankylophallus phanus* n. sp. Left gonopod, mesal aspect. Text-fig. 17. *Dromodesmus celer* n. sp. Left gonopod, mesal aspect. Text-fig. 18. *Liorhabdus beebei.* n. sp. Left gonopod, subanterior view. Text-fig. 19. *Liorhabdus beebei* n. sp. Left gonopod, ventral view. Text-fig. 20. *Orthomorpha watsa* n. sp. Distal end of gonopod. Text-fig. 21. *Orthomorpha coarctata* (Saussure). Distal end of gonopod.

**Rhinocricus acrotypus,** new species.

Text-figs. 9 & 10.

Characteristically marked with black or olive-black annuli which embrace most of the tergites above but narrow to a point down the sides and part way beneath; the remaining parts of each segment yellow in color, the yellow bands broad ventrally, where they fuse, and narrowing in a stripe across dorsum along the segmental border. Collum dark, with yellow or orange borders. Head dark above, with antennae orange or somewhat ferruginous. Legs ferruginous. Anal tergite light at caudal end only.

Head smooth; the median sulcus well developed and below but interrupted at middle as usual. Clypeal foveolae 2—2.

Metazonites smooth and shining above; the longitudinal sulci fine, incomplete in upper part of series. Striae of prozonite oblique and conspicuous on the sides; transverse, wavy and broken across dorsum. Anal tergite bluntly rounded behind. Inner border of anal valves but little protruding. Scobina with anterior lunate impressions strongly marked, separated by a little more than twice their width; striae fine, the area longer than wide, narrowly rounded behind; present back to about the fifth segment from the last.

Gonopods with apical part of sternite rather narrower, more set-off than in the other species here described. Posterior gonopods of the type usual in *Rhinocricus,* with details of distal branches as shown in Text-fig. 10. For form of anterior gonopods see Text-fig. 9.

Number of segments: 49 (♂) and 50 (♀).

Length of male holotype: about 66 mm.; width, 5 mm. Width of female allotype, 5.8 mm.

Locality: Venezuela: Caripito. A male and female taken in July.

This is the largest of the species here considered, among which it would seem to be readily distinguishable by its color pattern.

Material: Holotype No. 42488, Allotype No. 42489.

**Rhinocricus finitis,** new species.

Text-figs. 11 & 12.

A conspicuously banded form like *monilicornis,* the bands being alternately dark brown and whitish or light yellow, the light bands over the metazonites broader than the dark ones. Legs light ferruginous. Apical part of last tergite light in color.

A secondary sulcus in front of the primary one sharply defined across dorsum as in *monilicornis*. Longitudinal sulci on metazonites complete beneath but incomplete in upper part of series.

Anal tergite surpassing anal valves as in *acrotypus* and other species of the genus.

The gonopods closely resembling those of *monilicornis* except in proportions. The posterior gonopods proportionately shorter, with the lesser terminal branch broader in proportion to the principal blade. The sternite surpassing the coxal plates instead of having tips on the same level. See further Text-figs. 11 and 12.

Number of segments: 52, of which the three preceding the anal are legless in the male type.

Diameter: 2.66 mm.

Locality: Venezuela: Caripito. One male taken in July.

A smaller form than *monilicornis*, the diameters being to each other about as 2:3. The larger number of body segments is due chiefly to three legless segments at caudal end which are absent in specimens of *monilicornis* examined.

Material: Holotype No. 42487.

**Rhinocricus monilicornis** (Porat).

Text-figs. 7 & 8.

*Spirobolus monilicornis* Porat, 1876, *Bih. Svensk. vet.-Akad. Handl.*, 4(7):31.

Localities: Bermudas: Nonsuch Id. One male (#35,295). British Guiana: Kartabo. A male and female taken Mar. 4. Venezuela: Caripito. One female taken in July.

**Rhinocricus rubritypus,** new species.

Prozonites red above, deep brown or black below; entire metazonites blackish. Collum red, with black borders. Last tergite reddish or orange. Legs and antennae brown to nearly black.

Eyes twice their diameter apart; median sulcus across vertex and down face sharply impressed and complete. Clypeal foveolae 2—2.

Segmental sulcus angularly bent at level of pore. Both metazonites and prozonites smooth above, the prozonites wholly lacking the usual transverse striolations but with oblique striae beneath. The longitudinal striae of metazonites fine, extending up to level of pore. Scobina consisting of the usual lunate depression or pit followed by a slightly depressed area which narrows caudad and seems to be wholly without striae.

Last tergite angularly narrowed behind and considerably surpassing the valves.

Number of segments: 42.

Length: about 50 mm.; width, 6 mm.

Locality: Venezuela: Rancho Grande. One female taken April 23, 1945.

Material: Holotype No. 45464.

**Rhinocricus cocos** Chamberlin.

*Rhinocricus cocos* Chamberlin, 1947, *Proc. Acad. Nat. Sci. Phil.*, 99:38; *23, 28.

Locality: Cocos Is. Many specimens were taken on the *Arcturus* Expedition of 1925.

## Order Polydesmida.

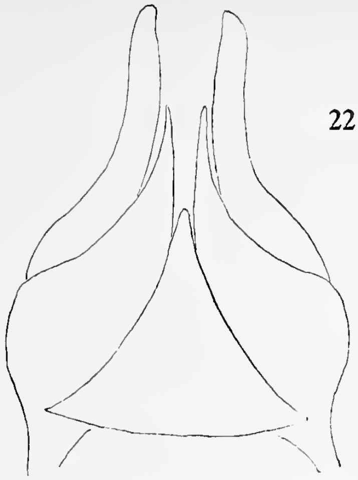
### Euryuridae.

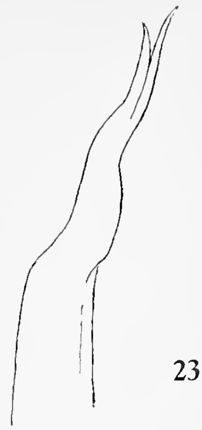
**Amplinus beebei,** new species.

Text-fig. 13.

Dorsum solid black. Legs and antennae brown.

Collum with four transverse series of strongly developed tubercles of which those




TEXT-FIG. 22. *Neocricus conclusus*, n. sp. Anterior gonopods. TEXT-FIG. 23. *Neocricus conclusus*, n. sp. Distal portion of posterior gonopod.

of caudal series are largest. All tubercles rounded and smooth. Succeeding tergites typically with three transverse series of elongate tubercles over the middle area, these breaking into four series of shorter tubercles on each side; some of the lateral tubercles, particularly the more posterior ones, more or less conically pointed but the median ones convexly rounded and smooth. Margins of keels thickened and elevated, with the pores conspicuously insunk. Caudal angles of keels produced and tending to be apically a little curved inwards.

In the gonopods the two branches are very unequal, the outer falcate, distally curving mesad well beyond the much shorter inner branch much as in *A. orphnius* of Honduras and Guatemala, but with the outer branch broader, more laminate, and the inner proportionately much shorter.

Length: about 58 mm.; width, 8.5 mm.

Locality: Venezuela: Rancho Grande. Several males and females taken during July and August on the jungle floor in "shrubs and trunks." Two were also taken in bromeliads.

Material: Holotype No. 461211, Paratypes No. 461212, No. 461216, No. 461217.

**Aphelidesmus confluens,** new species.

Text-fig. 14.

Dorsum dark chestnut, in part almost black, with the thickened borders of keels yellow. Legs yellow. Antennae yellow at base, becoming almost chestnut distally.

The collum with lateral ends narrowly obtusely rounded, not as much narrowed as in *frangens*.

Poriferous keels much swollen about pores, the borders much thicker than on the nonporiferous keels.

Sternites without processes.

Anal scale semicircular, convexly produced between the tubercles.

Gonopods obviously different from those of *frangens* and other related species. See Text-fig. 14 for details.

Width of male holotype: 4.2 mm.

Locality: Venezuela: Rancho Grande. The male holotype was taken April 22, 1945, and 11 paratypes in July-August, 1946.

Material: Holotype No. 45459, 11 Paratypes No. 4555.

**Aphelidesmus frangens,** new species.

Text-fig. 15.

General color of dorsum of female brown, with keels yellow. Legs lighter brown or yellowish. The male holotype is darker, nearly black.

Collum in the female conspicuously different from that of *hybridus* in having the keels more strongly narrowing down the sides, with the ends blunt or rounded, much narrower than the plate across dorsal line.

The thickened border developed almost as much on the keels lacking pores as on the poriferous ones.

Sternites not bearing paired tubercles at each lateral end; the fourth without pointed tubercles or processes. Second joint of legs not produced at end.

Anal scale in outline trapeziform, convexly produced between the setigerous tubercles.

Differing from other known species in the details of the male gonopods; e.g., in presenting on the posterior sub-basal portion of the tibio-tarsus a short but conspicuous laminate process. See further Text-fig. 15.

Width: 7.5 mm.

Locality: Venezuela: Rancho Grande. Male holotype and three females taken on jungle floor in July-August, 1946, by Dr. Beebe.

In type of gonopods suggesting *A. hermaphroditus* Brolemann, but aside from differences in details of those organs, it is a much larger form.

Material: Holotype No. 461214, 3 Paratypes No. 461230.

### Eurydesmidae.

**Ankylophallus phanus,** new species.

Text-fig. 16.

Dark chestnut, with the thickened borders of the keels bright yellow. Legs yellow and antennae light brown.

Collum wide, acutely narrowed toward each end, the lateral margin continuing evenly the curve of the anterior margin; but little depressed laterally.

Dorsum smooth and shining. Keels of the first four segments rather wide, in contact with each other, while the keels of the following segments are well separated, the prozonites being long. Keels behind the fourth segment narrow; caudal angles acutely produced; margins thickened, with the swelling about pores moderate. Tip of cauda moderately decurved, furcate or bidentate at end.

Legs long and slender distad of the second joint; third joint much longest, the fourth and fifth short, the latter in the male produced into a short ventral pad at distal end.

Gonopods of male as drawn (Text-fig. 16.)

Length: 37 mm.; width, 5.6 mm.

Locality: Venezuela: Rancho Grande. One male and two females taken during the week of March 22-29, 1945.

Material: Holotype No. 45460, 2 Paratypes No. 45461.

**Dromodesmus celer,** new species.

Text-fig. 17.

Dorsum chestnut to chocolate colored with the keels yellowish over laterocaudal portion. Antennae chestnut and the legs brown.

Head and prozonites densely finely granular. Collum with keels horizontal; with two rows of tubercles in front of caudal margin.

On tergites following the first the keels turn upward above level of dorsum and become conspicuously produced as in the generotype. Two transverse series of tubercles over caudal portion of tergite, the tubercles of the posterior row larger, and in front of suture an incomplete series. Basal half or more of keels densely tubercular, the outer portion nearly smooth.

Legs and antennae very long as in *longipes.*

Width: 4.6 mm.

Locality: Venezuela: Rancho Grande. One male, lacking the posterior end, was taken in July-August, 1946.

The generotype, *D. longipes* Chamberlin, was taken at Fundacion in Colombia. From that species the present one is readily distinguishable in the details of the gonopods as represented in Text-fig. 17.

Material: Holotype No. 461206.

**Liorhabdus,** new genus.

Closely related to *Cyclorhabdus* in having the tibio-tarsus of the male gonopods unsegmented and unbranched, being in the form of a simple, curved lamina which bears distally a slender process or style; mesal coxal laminae meeting at middle but not fused. A somewhat transitional genus differing from *Cyclorhabdus* in not having pads produced from end of first tarsal segment beneath the second, and in having long, acuminate processes from the coxae of the third legs of the male. No processes on sternite of fifth segment.

Generotype: *Liorhabdus beebei,* new species.

**Liorhabdus beebei,** new species.

Text-figs. 18 & 19.

Dorsum light brown, with an interrupted median dorsal yellow stripe, this distinct on prozonites but weaker on metazonites on which it ordinarily shows only on anterior part. Keels yellow. Head and collum deeper brown, the head lighter on face with clypeal region yellow. Antennae light brown proximally, with seventh joint and distal half of the sixth joint abruptly darker brown. Legs yellow.

Head smooth; vertigial sulcus fine but distinct; a pair of setae between bases of antennae and a second pair, a little more widely separated, below level of antennae. Antennae long, slender except sixth article which is clavately thickened distad; third and sixth joints somewhat the longest.

Collum large, its keels in line with those of following segments; smooth.

Surface of tergites smooth and glabrous. Keels of second and third segments with caudal corners rectangular, those of the following segments with the angles more and more produced caudad, the processes in middle and posterior regions prolonged and very acute; processes of the nineteenth tergite slender, parallel with body axis.

Second tarsal joint of legs proportionately longer than in the species of *Cyclorhabdus* and not supported by a pad beneath from preceding joint. In the male the coxal processes of the third legs are long, apically, conically pointed and curved forward. Coxae of sixth and seventh legs produced ventrad into conspicuous rounded prominences.

The gonopods of the male are as represented in Text-figs. 18 and 19.

Length: about 30 mm.; width, including keels, 4 mm.

Locality: Venezuela: Rancho Grande. One male taken by Dr. Beebe on July 25, 1948.

Material: Holotype No. 481563.

## Cryptodesmidae.

**Tunochilus,** new genus.

Collum nearly completely covering the head from above; anterior and lateral border upturned much as in *Pilochilus,* the anterior face of the upturned border nearly vertical and extending down to fit snugly against the head. The upturned border of collum not lobed as in *Pilochilus,* though widely and deeply notched at the middle line in front; the border above crossed by numerous fine ridges which project at free margin as denticles, these radial markings giving the

somewhat translucent outer part of the border a fluted appearance. The keels of the succeeding tergites also rising above level of the dorsum but becoming more nearly horizontal toward the posterior end; borders of keels crossed with radial fine ridges like those of collum, with the free margin similarly finely dentate or serrate. Pores dorsal in position, located within the fluted border on segments 5,7,9, 10(?), 12, 13 and 15 to 19. Caudal tergite well developed and freely exposed. Tergites densely finely tubercular and with two or three transverse series of subconical tubercles. Generotype: *Tunochilus marginis*, new species.

**Tunochilus marginis,** new species.

Dorsum brown, with the keels yellow.

Surface of the head finely granular. Antennal sockets rather close to each other. Antennae long and slender.

Collum covering the head above and fitting tightly against it; its anterior and lateral border turned conspicuously upward, the margin of the upturned rim finely serrate and with a large notch at middle line in front; level surface within the rim densely and finely granular; the clearer border of the rim without granules.

Keels of succeeding tergites upturned above level of intervening dorsum which is only slightly convex. Each tergite with a series of small but rather high, subconical, tubercles across caudal border, another series at middle, and an incomplete one farther forward; surface elsewhere finely granular; keels finely and unevenly serrate along free margins. Pores located a little more than their diameter from the inner edge of the striate border or three diameters from the outer margin.

Last tergite rather long, narrowing gently caudad, the end strongly convex; surface with numerous conical tubercles, some of which project along margins.

Width: 6 mm.

Locality: Venezuela: Rancho Grande. Two females taken in bromeliads on June 6, 1946.

Material: Holotype No. 461213.

PLATYRRHACIDAE.

**Rhyphodesmus kartabo,** new species.

Entire dorsum, including keels, brown.

Surface of head densely and rather coarsely granular. Vertigial sulcus distinct, ending in a transverse depression between the antennae.

Collum with surface densely covered with tubercles or coarse granules but with no definite series of larger tubercles.

The succeeding tergites have the keels depressed, the dorsum between them high and strongly convex; surface densely tubercular, the tubercles evenly distributed, with no definite series of larger tubercles, the tubercles extending to and upon the margins of the keels; pores about three times their diameter from the margin.

Last tergite semicircular, the lateral and caudal margins forming an even curve; surface covered with granules abruptly smaller than those of the preceding tergites.

Diameter: 13 mm.

Locality: British Guiana: Kartabo. One female.

Distinguished from *R. amphelictus*, another Guianan species, which it resembles in size and color, in lacking definite series of larger tubercles on dorsum, in having the pores more remote from the margins of the keels, and in the more strongly elevated, convex dorsum.

ONISCODESMIDAE.

**Oniscodesmus variegatus,** new species.

While material is not at hand for direct comparison, a reading of Brolemann's redescription of *O. aurantiacus* of Peters and of his own *O. aurantiacus villosus* indicates a close relationship to the latter but with significant differences. Like *villosus* the present species has the surface of the tergites finely shagreened and bearing hairs, but the latter are mostly short erect points only and by no means justifying the designation of villous attributed to the clothing of *villosus*.

The general color of the dorsum is reddish-brown, with irregular blacker areas as described for *villosus*. The anal tergite is solid black. The coloration of the head is characteristic, the vertex being black above the level of the antennal sockets and light gray elsewhere, the contrast between these areas being sharp. Antennae also gray proximally elsewhere becoming dark and showing an olive cast. Ventral surface of body reddish-yellow. Legs clear yellow.

Tergites above with the transverse sulcus well defined across dorsum and down to level of pores, with the narrower posterior division marked off by it considerably depressed below level of anterior portion and divided into areas by longitudinal sulci as in other species. The last tergite broad and much exposed, being overlapped anteriorly by the nineteenth tergite and laterally only a little by the keels of that segment.

A considerably larger form than *villosus*, having a width of 5 mm. as against less than 4 mm. given for the type of the latter.

Locality: Venezuela: Rancho Grande. One female taken during week of March 2-9, 1945.

Material: Holotype No. 45458.

**Oniscodesmus clarus,** new species.

Contrasting in color with *variegatus*, the color of the body being yellow to light brown throughout, with a series of dark slots on each side in line with bases of keels; last tergite nearly black above, the penult tergite also dusky. Head brown above and in front, with its sides clear yellow. Antennae yellow, proximally darker, and also brownish distally. Legs light yellow. Dorsum lacking the series of clear orange spots present in *aurantiacus*.

The collum is narrower at the ends than in *variegatus* and the other species mentioned, its width being more nearly uniform.

Surface of tergites mostly smooth. Some sparsely distributed, short hairs are detected.

Width: 4.5 mm. It is thus a little smaller than *variegatus* and a little larger than *aurantiacus*.

Locality: Venezuela: Rancho Grande. One specimen taken in May-June, 1946.

Material: Holotype No. 461205.

STRONGYLOSOMIDAE.

**Orthomorpha watsa,** new species.

Text-fig. 20.

Dorsum chestnut, the keels yellow. Legs yellow.

Head roughened over vertex and down to level of antennae; not pilose. Antennae rather long, clavately thickened distad.

Sternite of fourth segment of male without process.

Keels all well developed, with caudal corners acutely produced.

Collum with lateral ends free; dorsal surface more or less obscurely rugose or tubercular.

Keels of second segment with caudal corners acutely produced those on posterior segment strongly so. Keels of the following segments large, the dorsum bteween them convex. Pores lateral in position, each on the lateral thickening well toward its ventral edge.

Anal tergite rather broad, the well separated terminal tubercles a little decurved.

Like *coarctata* in lacking sternal processes, but differing in the form of the gonopods, which are represented in Text-fig. 20 with which Text-fig. 21, representing the corresponding part of the gonopod of *coarctata*, may be compared.

Length: up to about 16 mm.; width, 2—2.2 mm.

Locality: British Guiana: Kartabo. Several specimens taken April 16.

Material. Holotype No. 241051.

# 11.

# The Relative Position of the Cetacea Among the Orders of Mammalia as Indicated by Precipitin Tests.

ALAN BOYDEN & DOUGLAS GEMEROY.

*Department of Zoology and Bureau of Biological Research, Rutgers University.*

(Text-figure 1).

There are still many unsolved problems in regard to the proper systematic positions of species, genera, families and orders of mammals. A reading of the frank and critical statements made by G. G. Simpson (1945) in his excellent report, "The principles of classification and a classification of mammals," will indicate the nature of some of the difficulties and the extent and diversity of these problems. With reference to the Cetacea, Simpson wrote as follows: (*loc. cit.*, p. 213-214):

"Because of their perfected adaptation to a completely aquatic life, with all its attendant conditions of respiration, circulation, dentition, locomotion, etc., the cetaceans are on the whole the most peculiar and aberrant of mammals. Their place in the sequence of cohorts and orders is open to question and is indeed quite impossible to determine in any purely objective way. There is no proper place for them in a *scala naturae* or in the necessarily one-dimensional sequence of a written classification. Because of their strong specialization, they might be placed at the end, but this would remove them far from any possible ancestral or related forms and might be taken to imply that they are the culmination of the Mammalia or the highest mammals instead of merely being the most atypical. A position at the beginning of the eutherian series would be even more misleading. They are, therefore, inserted into this series in a more or less parenthetical sense. They may be imagined as extending into a different dimension from any of the surrounding orders and cohorts."

It was this statement which stimulated us to undertake a careful comparison of the reactions of whale sera with those of other mammals, using a modern quantitative precipitin technique. Our hope was that evidence bearing upon the relative position of the Cetacea to other orders of mammals might thus be obtained, which, under the circumstances, could be of decisive importance.

## MATERIALS AND METHODS.

### ANTIGENS.

Sera or protein fractions of sera representing 17[1] of the 18 existing orders of mammals listed by Simpson (1945) have been tested. These sera have come from many parts of the world and have been obtained through the aid of many individuals and institutions. A list of contributing agents and agencies may be found under "Acknowledgments."

These sera have had various treatments and histories. The following kinds of materials were used for the production of suitable antisera, or for testing, or for both purposes.

1. Native fluid sera, Seitz filtered and stored in refrigerator.
2. Native sera kept frozen and then melted, Seitz filtered and stored in refrigerator.
3. Fluid sera preserved with formalin at a final concentration of 0.2% formalin.
4. Fluid sera preserved with merthiolate at a final concentration of 1:10,000.
5. Plasma with sodium citrate or oxalate, Seitz filtered.
6. Lyophilized sera redissolved and Seitz filtered.
7. Purified fractions of sera, Seitz filtered.
8. Lyophilized sera extracted with Bloor's mixture, redissolved in saline and Seitz filtered.

In regard to the extracted sera the procedure was as follows:

Lyophilized serum was extracted with Bloor's mixture (absolute ethyl ether 3 parts and absolute ethyl alcohol 1 part by volume) using 100 ml. of extractant to each gm. of dried protein. The suspension of protein in extractant was shaken 1 hour in the shaking machine and then allowed to settle out overnight in the refrigerator. Next day the clear supernatant was siphoned off and a new lot of extractant was added, to be followed by a similar shaking and settling period. Three such extractions were carried out followed by the collection of the suspended protein on filter paper and its rapid drying under vacuum. When all the Bloor's mixture had

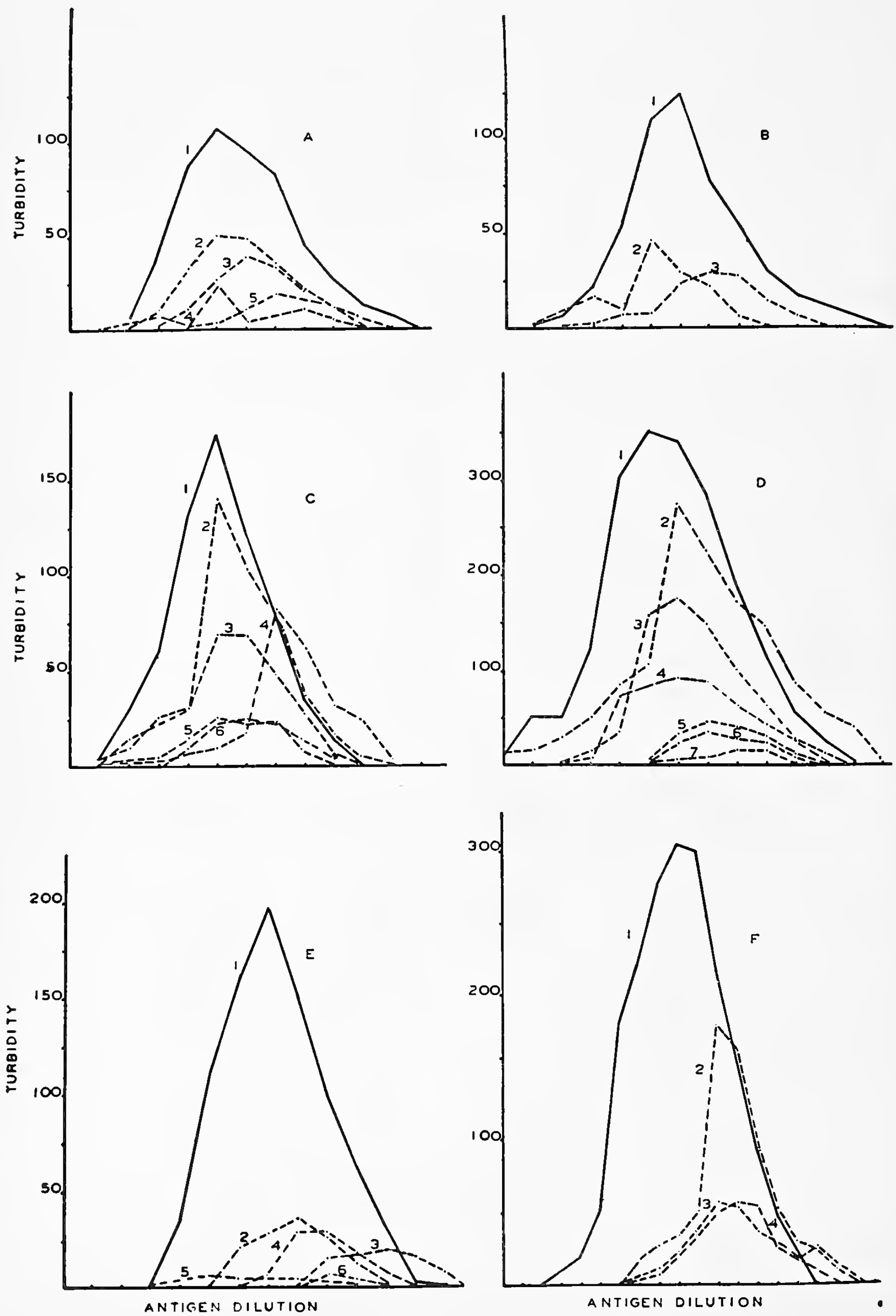
[1] The fact that the antisera employed were made in rabbits automatically removes the order Lagomorpha from the direct comparisons.

been removed the dried protein was redissolved in saline and Seitz filtered.

The purified bovine albumin and fraction II of bovine globulin were obtained from the Armour Laboratories and made up in solutions of appropriate strength for use, viz., about 5%.

ANTISERA.

Sixty-five antisera representing 14 mammalian orders have provided the foci from which a many-sided view of the systematic position of the whales was obtained. All of these antisera were produced in rabbits and most of them by a "presensitization" method. In this procedure a rabbit is given a single injection of 1 ml. of some serum or other antigen, intravenously or subcutaneously, followed by a rest period of 3 or 4 weeks. Thereafter a series of 4 subcutaneous injec-



tions of antigen follows, 1 ml. being given on each alternate day. Seven days after the last injection a trial bleeding is made, and if the antiserum is sufficiently powerful the rabbit is bled out rapidly by cardiac puncture with a 50 ml. syringe, the following day. Food is withheld for 24 hours prior to the bleeding. The blood is allowed to clot in small tubes, kept at room temperature for an hour or two and then placed in the ice chest. Centrifuging may follow later the same day or the next day. The clear antiserum is Seitz filtered and stored in the refrigerator.

If the first series of injections did not give a sufficiently powerful antiserum, additional series may be given. In the case of bovine albumin, alum precipitation was regularly practiced. By these procedures powerful broad-ranging antisera were usually obtained, suitable for the interordinal comparisons.

## Testing Procedures

The methods used in making the precipitin tests have been described by Boyden & DeFalco (1943). The validity of such testing procedures involving the Libby Photronreflectometer has been further demonstrated in the reports of Boyden, Bolton & Gemeroy (1947) and Bolton, Leone & Boyden (1948).

## Results of the Comparisons.

Table I with its various subdivisions shows the results of the comparisons between the Artiodactyla and Cetacea. Text-figure 1 shows graphically a small but representative selection of some of the curves resulting from the tests bearing upon the relations of the Artiodactyla and Cetacea with each other and with other orders also. The table is subdivided in accordance with the nature of the antigens and antisera and most of the tests are corresponding in the sense

Text-Figure 1. The reaction of six antisera with a variety of antigens.

In each graph the relative turbidities as measured with the Libby Photronreflectometer are plotted along the ordinates and the successive antigen dilutions are plotted along the abscissas. The zone of antigen excess lies in all cases to the left of the peaks of the curves. Each successive antigen dilution contains half the concentration of its immediate predecessor. The relative areas under the curves are determined by summing the ordinates, and the homologous area is the standard of reference for each graph, rated at 100 per cent.

| | | Area | Per cent. |
|---|---|---|---|
| Graph A Anti-Fin Whale CFo (No. 213) | | | |
| Tested with | (1) Fin Whale CFo | 579 | 100 |
| | (2) Sperm Whale 48-3Fo | 214 | 37 |
| | (3) Sperm Whale 48-2Fo | 147 | 25 |
| | (4) Beef R4Fo | 85 | 15 |
| | (5) Pig 45-3CFo | 72 | 12 |
| Graph B Anti-Fin Whale CFo (No. 214) | | | |
| Tested with | (1) Fin Whale CFo | 519 | 100 |
| | (2) Beef R4Fo | 149 | 29 |
| | (3) Lyo-beef 47-6Fo | 120 | 23 |
| Graph C Anti-lyosheep 47-1 (No. 209) | | | |
| Tested with | (1) Lyosheep 47-1 | 647 | 100 |
| | (2) Lyobeef 47-6 | 457 | 71 |
| | (3) Giraffe 43-1 | 294 | 45 |
| | (4) Beef Albumin 47-1 | 247 | 38 |
| | (5) Fin Whale CFo | 109 | 17 |
| | (6) Pigmy Sperm Whale 48-1ME | 95 | 15 |
| Graph D Anti-lyobeef (No. 201) | | | |
| Tested with | (1) Lyobeef 47-3 | 1904 | 100 |
| | (2) Beef Albumin 47-1 | 1285 | 67 |
| | (3) Pigmy Sperm Whale 48-1ME | 721 | 38 |
| | (4) Fin Whale CFo | 528 | 28 |
| | (5) Coyote Ro78 | 160 | 8 |
| | (6) Rhesus II | 145 | 8 |
| | (7) Elephant Goss 19 | 39 | 2 |
| Graph E Anti-ext. Fin Whale 48-9 (No. 197) | | | |
| Tested with | (1) Fin Whale 48-9 | 853 | 100 |
| | (2) Lyobeef 48-1 | 130 | 15 |
| | (3) Beef Albumin 45-1 | 81 | 9 |
| | (4) Kudu 48-1 | 92 | 11 |
| | (5) Hedgehog 19-8-48 | 37 | 4 |
| | (6) Giant Pangolin 1011 | 14 | 2 |
| Graph F Anti-ext. Beef 47-1Fo (No. 233) | | | |
| Tested with | (1) Ext. Beef 47-1Fo | 1906 | 100 |
| | (2) Beef Albumin 47-1Fo | 674 | 35 |
| | (3) Fin Whale CFo | 284 | 15 |
| | (4) Pigmy Sperm Whale 48-1MEFo | 333 | 17 |

## TABLE I.

Summary of Values: Artiodactyla vs. Cetacea.

A. ANTINATIVE ARTIODACTYL SERUM × NATIVE WHALE SERUM.

| Antiserum | Kind | Homologous Area | Heterologous Area | Kind | Per cent. Heterol. Area / Homol. Area |
|---|---|---|---|---|---|
| 41 | Lyobeef[2] | 2135 | 309 | Pigmy Sperm 48-1 ME | 15 |
| 42 | Lyobeef[2] | 1272 | 146 | Pigmy Sperm 48-1 ME | 12 |
| 44 | Lyobeef[2] | 980 | 64 | Pigmy Sperm 48-1 ME | 7 |
| 45 | Lyobeef[2] | 883 | 170 | Pigmy Sperm 48-1 ME | 19 |
| 47 | Lyobeef[2] | 1624 | 59 | Pigmy Sperm 48-1 ME | 4 |
| 52 | Lyobeef[2] | 1745 | 94 | Pigmy Sperm 48-1 ME | 5 |
| 53 | Lyobeef[2] | 194 | 4 | Pigmy Sperm 48-1 ME | 2 |
| 54 | Lyobeef[2] | 1220 | 10 | Pigmy Sperm 48-1 ME | 1 |
| 55 | Lyobeef[2] | 1073 | 24 | Pigmy Sperm 48-1 ME | 2 |
| 56 | Lyobeef[2] | 1602 | 85 | Pigmy Sperm 48-1 ME | 5 |
| 60 | Lyobeef[2] | 1254 | 135 | Pigmy Sperm 48-1 ME | 11 |
| 63 | Lyobeef[2] | 2522 | 929 | Pigmy Sperm 48-1 ME | 37[3] |
| 65 | Lyobeef[2] | 1978 | 554 | Pigmy Sperm 48-1 ME | 28[3] |
| 201 | Lyobeef[2] | 1904 | 721 | Pigmy Sperm 48-1 ME | 38[3] |
| 202 | Lyobeef[2] | 1383 | 83 | Pigmy Sperm 48-1 ME | 6 |
| 209 | Sheep | 647 | 95 | Pigmy Sperm 48-1 ME | 15 |
| 210 | Sheep | 898 | 0 | Pigmy Sperm 48-1 ME | 0 |
| 228 | Warthog | 1708 | 240 | Pigmy Sperm 48-1 ME | 14 |
| 229 | Warthog | 1055 | 34 | Pigmy Sperm 48-1 ME | 3 |
| 255 | Kudu | 2085 | 159 | Pigmy Sperm 48-1 ME | 8 |
| 256 | Kudu | 1595 | 218 | Pigmy Sperm 48-1 ME | 14 |
| | | | | Average | 8.9% |

[2] The scientific names corresponding to the common names which appear in the table are as follows:

| | |
|---|---|
| Beef | *Bos taurus* |
| Sheep | *Ovis aries* |
| Warthog | *Phacochoerus* sp. |
| Kudu | *Tragelaphus kudu* |
| Bison | *Bison bison* |
| Pig | *Sus scrofa* |
| Pigmy Sperm Whale | *Kogia breviceps* |
| Fin Whale | *Balaenoptera physalus* |
| Sperm Whale | *Physeter catodon* |

[3] These values, unusually high for even the inordinal tests of Artiodactyla and Cetacea, have not been included in the average. Further comment regarding them is to be found under the section dealing with the effect of proportion of anti-albumins to total anti-body on the relationship values.

that antinative sera are tested with native sera, or antiformolized sera are tested with formolized sera. The average of all tests in Table I was 10.9%, a substantial value for interordinal tests, to be compared with the value of 1.9% for all other interordinal comparisons made.

Examining the subdivisions of Table I we find that the average value for the comparisons involving native sera was 8.9% (excluding the 3 values for antisera #63, 65, 201, which are treated separately); for the comparisons involving formolized antigens it was 13.2%; for the comparisons involving antisera to extracted antigens it was 9.0%; and, finally, for the comparisons involving antisera to particular bovine fractions it was 8.2%.

Out of the 65 sets of curves available, a small sample involving six antisera is shown in Text-figure 1. All the curves belong to the same general type; in fact this is true regardless of the kind of antigen and antiserum used.

The first tests in this investigation were made with the antisera shown in the upper two graphs (A & B) of Text-figure 1. These were anti-fin whale sera. The first heterologous tests made with these antisera were with beef serum and the surprisingly strong reactions gave us the clue which has been followed to a logical conclusion. These tests were made with antisera to formolized antigens tested with formolized antigens.

Charts C and D of Text-figure 1 show the results of testing antisera made to lyophilized sera. In chart C, an antisheep serum was tested with sheep, beef and giraffe sera, and with beef albumin, to show the magnitudes of the artiodactylan reactions in comparison with those of the cetaceans. "Fin whale C" serum was available only as formolized antigen.

Graph D illustrates the results of testing an antibeef serum with a variety of antigens of several orders. This antiserum contained an unusually high proportion of anti-albumins and gives generally higher heterologous values than do antisera with lower relative amounts of anti-albumins.

Graphs E and F illustrate the reactions obtained with antisera made to extracted antigens. E shows the results of testing an anti-fin whale serum with representatives of the Artiodactyla, Insectivora and Pholidota. F shows the results of testing antibeef serum made to extracted and formolized beef serum with formolized whale sera and to formolized beef albumin. The cetacean-

TABLE I (continued).

B. ANTIFORMOLIZED SERA × FORMOLIZED SERA.

| Antiserum | Kind | Homologous Area | Heterologous Area | Kind | Per cent. Heterol. Area / Homol. Area |
|---|---|---|---|---|---|
| 213 | Fin Whale C Fo | 579 | 85 | Beef R4 Fo | 15 |
| | C Fo | 579 | 35 | Bison Ro17 Fo | 6 |
| | C Fo | 579 | 72 | Pig 45-3c Fo | 12 |
| 214 | C Fo | 519 | 149 | Beef R4 Fo | 29 |
| | C Fo | 519 | 120 | Lyobeef 47-6 Fo | 23 |
| | C Fo | 519 | 32 | Bison Ro17 Fo | 6 |
| | C Fo | 519 | 23 | Longhorn Ro18 Fo | 4 |
| | C Fo | 519 | 49 | Pig 45-3c Fo | 9 |
| 234 | Lyobeef Fo | 1789 | 309 | Pigmy Sperm 48-1 ME Fo | 17 |
| | Lyobeef Fo | 1789 | 205 | Fin Whale C Fo | 11 |
| | | | | Average | 13.2% |

C. ANTI-EXTRACTED SERA × NATIVE OR FORMOLIZED SERA.

| Antiserum | Kind | Homologous Area | Heterologous Area | Kind | Per cent. Heterol. Area / Homol. Area |
|---|---|---|---|---|---|
| 197 | Ext. Fin Whale | 853 | 130 | Lyobeef 48-1 | 15 |
| | Ext. Fin Whale | 853 | 92 | Kudu 48-1 | 11 |
| | Ext. Fin Whale | 853 | 0 | Warthog Goss 47-Z2 | 0 |
| 198 | Ext. Fin Whale | 918 | 60 | Lyobeef 48-1 | 7 |
| 199 | Ext. Fin Whale | 835 | 119 | Lyobeef 48-1 | 14 |
| 205 | Ext. Lyobeef | 753 | 44 | Pigmy Sperm 48-1 ME | 6 |
| 206 | Ext. Lyobeef | 2040 | 158 | Pigmy Sperm 48-1 ME | 8 |
| 211 | Ext. Lyosheep | 1360 | 43 | Pigmy Sperm 48-1 ME | 3 |
| 212 | Ext. Lyosheep | 1454 | 31 | Pigmy Sperm 48-1 ME | 2 |
| 233 | Ext. Beef Fo | 1906 | 333 | Pigmy Sperm ME Fo | 17 |
| 233 | Ext. Beef Fo | 1906 | 294 | Fin Whale C Fo | 15 |
| | | | | Average | 9.0% |

D. ANTIBOVINE FRACTIONS × NATIVE OR FORMOLIZED WHALE SERA.

| Antiserum | Kind | Homologous Area | Heterologous Area | Kind | Per cent. Heterol. Area / Homol. Area |
|---|---|---|---|---|---|
| 2 | Anti-albumin | 1573 | 92 | Fin Whale C Fo | 6 |
| 246 | Anti-albumin | 2239 | 409 | Pigmy Sperm 48-1 ME | 18 |
| 257 | Anti-albumin Fo | 1022 | 107 | Pigmy Sperm 48-1 ME Fo | 10 |
| 257 | Anti-albumin Fo | 1022 | 50 | Fin Whale C Fo | 5 |
| 3 | Globulin II | 779 | 0 | Fin Whale C Fo | 0 |
| 237 | Globulin II | 1307 | 133 | Pigmy Sperm 48-1 ME | 10 |
| | | | | Average | 8.2% |

artiodactylan relationships shown in graphs E and F are typical values.

The data given in the table and graphs serve as the basis for the following tentative conclusions:

(1) The tests involving formolized antigens, and antisera made to them, appear to give somewhat higher average values than the remaining tests.

(2) The values obtained with extracted antigens and antisera made to them, or with purified fractions and their corresponding antisera, are not significantly different from the values based on native comparisons. There is no evidence therefore that lipoidal materials have affected the values significantly.

(3) Of the values obtained with purified antigens shown in Table I, D, those based on the albumins give a higher average (10%) than those based on the globulins (5%).

(4) There is considerable variability in the individual values shown throughout, a fact which needs further analysis and explanation.

## DISCUSSION.

Some explanation of the variability of results obtained when different antisera of the same kind are tested is needed. Every rabbit responds as an individual to the treatment with an antigen, and produces antibodies of amounts and kinds in accordance with its inherent physiological capacity. The antisera so produced by different rabbits may vary (1) in their strength, i.e., their antibody content; (2) in their sensitivity, i.e., in their capacity to react with minimal amounts of antigen; (3) in their range, which is the capacity to react with distantly related or chemically diverse antigens; (4) in their specificity, which is their capacity to react differentially with a variety of antigens; and (5) in the numbers and proportions of the different kinds of antibody produced to serologically distinct antigens. With such possibilities of variation among antisera of the same kind, i.e., produced to the same composite antigen, the amazing thing is the relatively great consistency of the results, for some rabbits were given but a

single injection series, and others two or three injection series, following the original presensitization. That this variation in injection procedure affects the range and specificity of the reactions with antisera made to mammalian sera is probably true.

In addition to other causes of variability in the relationship values than those hitherto discovered, we find that the proportion of anti-albumins to total antibodies in the antiserum seems to be highly significant. Thus the three antisera listed in Table I, A, with highest relationship values (#63, 65 and 201) belong in a class by themselves, having 67 to 70% of anti-albumins, whereas the anti-albumin content of 16 other antibovine sera varied from 0 to 45% with an average of 20%. Again, the anti-albumin tests in Table I, D, gave an average value which was about double the value for the globulin II tests. These data may be interpreted to mean that the albumins of the Artiodactyla and Cetacea are more similar than their globulins and have been more conservatively evolved. If this conclusion is justified in these comparisons, it may hold for mammalian comparisons in general, and our preliminary tests indicate that this is true. If so, an important additional source of variability in the magnitude of relationship values has been discovered, to be reckoned with in the future. It may well be that the anti $\frac{A}{G}$ ratio for antisera produced to vertebrate sera, which are mixed antigens, will become as significant in systematic serology as the $\frac{A}{G}$ ratio is in general physiology. The analysis of the anti-albumin content of these 19 antibovine sera was made relatively easy by the availability of purified bovine albumins obtained through the Armour Laboratories.

The order of magnitude of some of the tests involving the Cetacea and other orders of mammals except the Artiodactyla is shown in the text-figure. The average of 59 such tests made with antisera to 13 orders and antigens representative of 16 orders of mammals was 2.1% .These interordinal tests involved the Cetacea compared with one or more representatives of the Monotremata, Marsupialia, Insectivora, Chiroptera, Dermoptera, Primates, Edentata, Pholidota, Rodentia, Carnivora, Tubulidentata, Proboscidea, Hyracoidea, Sirenia and Perissodactyla.

The average interordinal value of 2.1% between the Cetacea and other orders, except the Artiodactyla, is of the same order of magnitude as the average value of interordinal tests between the Artiodactyla and the other orders exclusive of Cetacea, or among a variety of other orders excluding Artiodactyla and Cetacea. This average value was 1.6%, involving 44 tests and 15 orders. Of course the Lagomorpha cannot be placed in these interordinal comparisons because the antisera were all produced by rabbits. It is true that some orders were necessarily represented by single species, because additional species or samples were unavailable. It is true also that not as many antisera were made to the orders other than Artiodactyla and Cetacea as to these two orders, but there has been no hint of values consistently high enough to warrant further testing.

Taken as they are the data justify the conclusion that the serum proteins and especially the albumins of Artiodactyla and Cetacea are more similar than the corresponding proteins of the other orders tested, and presumably therefore the Cetacea and Artiodactyla have a closer blood and genetic relationship than the other orders do. The significance of these conclusions may be discussed for some time to come.

The various conflicting views and interpretations of the morphological evidences regarding cetacean relationships are presented in full to that time in Kellogg's report, "A Review of the Archaeoceti" (1936). Kellogg tentatively concludes that the Cetacea have descended from some primitive insectivore-creodont ancestry of long ago, admitting the inadequacy of the morphological evidences to settle the question. As previously stated, Simpson (1945) finds the evidences too uncertain to permit of any definite placement of the Cetacea. The report of H. W. Mossman (1937) on "Comparative Morphogenesis of the Fetal Membranes and Accessory Uterine Structures" places the Cetacea and Artiodactyla together as derivatives of a primitive ungulate stock. This interpretation accords very well with ours based on the blood tests.

We have provided evidence (Boyden, 1942; Boyden, Gemeroy & Bolton, 1949) that the serum tests accord with genetic relationships where they are known, as in the relation of mule and hinny to horse and ass. There is also considerable evidence that precipitin tests accord well with systematic relationships among close relatives or where the systematic positions are fairly well established. This is true for Crustacea (Boyden, 1943) Insecta (Leone, 1947 a and b) Pisces (Gemeroy, 1943) Amphibia (Boyden & Noble, 1933) Aves (DeFalco, 1942) and Mammalia (Boyden, 1926, 1942), (Boyden & DeFalco, 1943).

In such a problem as that of the systematic position of the whales, where the morphological evidences are inconclusive and inadequate, other sources of information are needed. Under these conditions the serological reactions may fill this need and provide evidence of a decisive nature.

## Summary.

Powerful precipitating antisera have been used to test the serological relationships of the Cetacea to the other orders of mammals. The interordinal reactions as determined by the quantitative photoelectric technique using the Libby Photronreflectometer are generally weak, averaging about 2%, with the exception that the artiodactyl-cetacean

comparisons are distinctly higher, averaging about 11%. The tests therefore indicate that there is a greater similarity in the serum proteins of representative Cetacea and Artiodactyla than between the Cetacea and any other orders tested, all existing orders but the Lagomorpha being included in the comparisons. Furthermore the tests indicate that there is a relatively greater similarity of the serum albumins of these two orders than of their globulins. The conclusions are therefore drawn that the Cetacea should be granted a greater degree of systematic relationship to the Artiodactyla than to any of the other mammalian orders tested and that the albumins of the sera of these two orders have been more conservatively evolved than their globulins.

## Acknowledgments.

Some of the sera used in these comparisons were collected or contributed prior to the creation of the Serological Museum (February 2, 1948) and some subsequently. Our thanks and appreciation for various samples used in the comparisons are extended to the following individuals and institutions:

Drs. Richard Barnes and Robert Pennell, and the Sharp & Dohme Laboratories, Glenolden, Pennsylvania.

Dr. Robert A. M. Case and the R. N. Physiol. Laboratory, Alverstoke, Hants, England.

Dr. E. J. Cohn, Harvard Medical School, Harvard University.

Dr. Paul R. Crimp and the Plymouth Laboratory of the Marine Biological Association.

Dr. F. C. Fraser and the British Museum of Natural History.

Dr. L. J. Goss and the New York Zoological Society.

Col. A. E. Hamerton and Dr. R. E. Rewell, and the Zoological Society of London.

Dr. L. Lachat and the Armour Laboratories, Chicago, Illinois.

Dr. Arthur F. McBride and the Marine Studios, Marineland, Florida.

Dr. C. M. Pomerat and the Medical Branch, University of Texas.

Dr. Joseph Pearson and the Tasmanian Museum. Hobart, Tasmania.

Dr. Victor Scheffer and the U. S. Fish and Wildlife Service.

Dr. J. G. Sharp and the Low Temperature Research Station, Cambridge University, England.

Messrs. James R. Simon and C. T. Wemyss, and the Jackson Hole Wildlife Park.

Dean L. B. Uichanco, College of Agriculture; Drs. H. A. Lara and P. R. Aragon of the Institute of Hygiene, and Mr. N. L. Denoga, Land Grant Administrator, all of the University of the Philippines, Manila, P. I.

Dr. Louis Van den Berghe and the Institut pour la Recherche Scientifique en Afrique Centrale.

## Literature Cited.

Bolton, E. T., C. A. Leone & A. A. Boyden.
1948. *Jour. Immunol.*, 58:169-181.

Boyden, A. A.
1926. *Biol. Bull.*, 50:73-107.
1942. *Physiol. Zool.*, 15:109-145.
1943. *Amer. Nat.*, 77:234-255.

Boyden, A. A., E. T. Bolton & D. G. Gemeroy.
1947. *Jour. Immunol.*, 57:211-227.

Boyden, A. A. & R. J. DeFalco.
1943. *Physiol. Zool.*, 16:229-241.

Boyden, A. A., D. G. Gemeroy & E. T. Bolton.
1949. *Proc. Eighth Intern. Cong. of Genetics*, p. 540-541.

Boyden, A. A. & G. K. Noble.
1933. *Amer. Mus. Novitates.*, No. 606.

DeFalco, R. J.
1942. *Biol. Bull.*, 83:205-218.

Gemeroy, D. G.
1943. *Zoologica*, 28:109-123.

Kellogg, R.
1936. *Carnegie Inst. of Wash. Pub. No.* 482.

Leone, C. A.
1947. *Biol. Bull.*, 93:67-71.
1947. *Ann. Entom. Soc. Amer.*, 40:417-433.

Mossman, H. W.
1937. *Carnegie Inst. Wash. Pub. No.* 479.

Simpson, G. G.
1945. *Bull. Amer. Mus. Nat. Hist.*, 85:1-350.

# ZOOLOGICA

SCIENTIFIC CONTRIBUTIONS
*of the*
NEW YORK ZOOLOGICAL SOCIETY

---

VOLUME 35
Part 3
Numbers 12-18

---



Published by the Society
The Zoological Park, New York
November 27, 1950

# CONTENTS

# 12.

# Factors Influencing the Establishment of Residence in Shells by Tropical Shore Fishes.

C. M. Breder, Jr.
*The American Museum of Natural History.*

(Plates I & II; Text-figures 1-5).

## Introduction.

A considerable variety of small tropical shore fishes establish more or less permanent residence in empty shells or similar cavities. Many maintain a proprietary attitude toward the territory immediately surrounding their place of abode, and not infrequently modify their area of activity by excavational or other means. Prominent among such shore fishes are *Pomacentrus leucostictus* Muller and Troschel and *Bathygobius soporator* (Cuvier and Valenciennes). Both species are abundant at Bimini where these studies were carried out at the Lerner Marine Laboratory during 1948 and 1949. Reasons were sought for the selective activity of these fishes, their method of recognizing home grounds and the general basic nature of the relationship of the individuals to these elements in their environment with which they have such intimate and continued contact. Both are vigorous in defense of their territories but differ notably in the rhythm of their activities. *Pomacentrus* is strictly diurnal and spends the dark hours completely hidden within the cavity of its selection, as has been indicated by Longley and Hildebrand (1941) and Breder (1948). *Bathygobius* on the other hand is active both during the daylight and dark periods.

In a suitable aquarium both species will accept practically any cavity offered as a place of retreat and after a period of establishment will defend their territory, which usually includes the whole aquarium floor, against all comers. For this reason the number that may be successfully kept in a small aquarium is sharply restricted because of fighting which frequently results, especially in the case of *Pomacentrus*, in the death of all but the dominant fish.

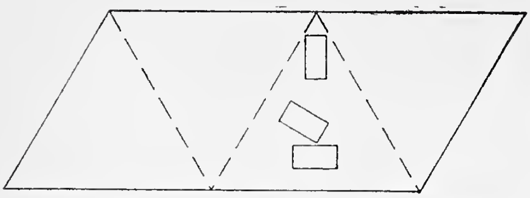
Although not closely related, there are many points of resemblance in the behavior of these two species. For example in modifying their environment both will excavate sand by fanning it away with their tails. *Pomacentrus* will often "fan" away marauding small invertebrates with more or less success while *Bathygobius* is more given to direct oral attack under similar conditions. Both will at times evince very definite reactions to an object moved from its accustomed place and if it is possible *Pomacentrus* will often return it repeatedly to its original site. This behavior was very well demonstrated in one aquarium containing a single mature *Pomacentrus*. A glass tube attached to a flexible rubber tube fed water to the aquarium and rested diagonally across the tank with its end resting on the bottom. If this tube was moved from a certain position it was always returned to it by the fish, frequently immediately, but always in at least 15 minutes. The fish would swim around the tube as though "studying" the situation and finally press its mouth against the tube and swim vigorously, replacing the tube to a position against one wall of the aquarium. This was close to the limits of physical ability of the fish and not infrequently as many as three separate attacks were necessary to replace the tube to the "desired" spot.

With material showing behavior as above outlined it would be expected that some of the reactions would be found to be fairly complex. The present contribution is to be considered an initial attempt to distinguish some of the elements comprising these reactions.

## Experimental Procedures.

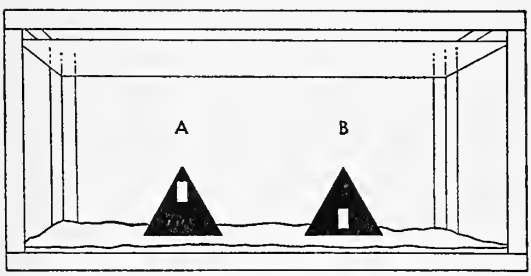
Since the shells inhabited by these fishes (most often *Strombus*) are fairly complicated forms in a physical sense it was thought that perhaps a simplifying of the form of the shelter would make it possible to understand more clearly the basic nature of some of the behavior. To this end a number of tetrahedrons were made of cardboard with a suitable opening as shown in Text-fig. 1. Some were prepared of black cardboard and some of white. With these as the only fittings in the aquaria, which measured 2′ × 1′ × 1′, the following experiments were undertaken.

Experiment 1. Two newly caught *Pomacentrus* about 1 inch in length and as nearly identical in coloration as possible were placed in an aquarium with two black tetrahedrons as shown in Text-fig. 2 on August 2. One fish discovered the opening in "B" in about five minutes but did not enter, simply hovering



Text-fig. 1. Pattern for the cardboard tetrahedrons. Three openings are indicated, only one of which was used in any one shelter. The altitude of each triangular face is 4 inches. The cut edges were bound with transparent Scotch tape.

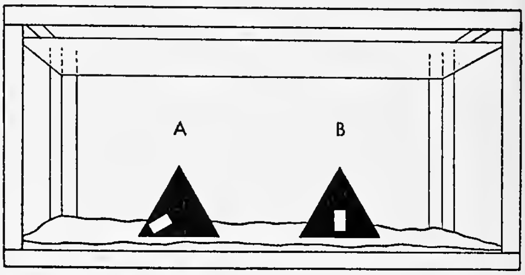
about and "examining" it. In these black tetrahedrons the opening becomes nearly invisible since the surface reflection of the cardboard largely disappears under water, except for the following condition in tetrahedron "B." Both had a small quantity of sand placed in them in order to insure their stability. Thus the one with the lower hole showed white through the opening while "A" with the upper hole did not. After about 20 minutes the fish entered "B" and seemed to accept and take possession of it. The other individual hovered about "A" at this time but evidently had not found the entrance.




Text-fig. 2. First arrangement of tetrahedrons in experiment 1.

One hour later the fish which established itself in "B" found the entrance in "A" and took possession of this as well. By now it was clear that this fish was definitely dominant over the other, which was not permitted near either of the tetrahedrons. The general situation at this time is shown in Plate I, Fig. 1. This condition was continued through the following day with no change of status. On the third day the tetrahedron "A" was changed in position as indicated in Text-fig. 3. While this change was being made the resident fish hid in "B" and as a consequence could not see the shift of position. Because of the nature of the geometrical figure used the only optically detectable change would be that of the place of the entrance. When the resident came out of "B" it swam to the place of the entrance of "A" before the shift. It momentarily stood there and then fled to hide in "B" again. In a short time it emerged and in about five minutes it found the new place of the entrance and from then on used it freely as shown in Plate I, Fig. 2. This continued for five days after which the experiment was terminated. Although these fish used these cardboard boxes freely, as described, on the coming of nightfall they would leave them and spend the night resting in the corners of the aquarium. A shell, on the other hand, is always occupied at night.

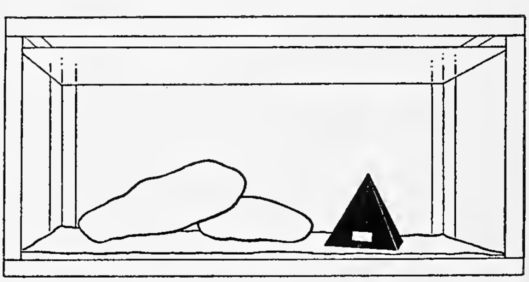
Experiment 2. On August 4, with two new but similar-sized *Pomacentrus*, another aquarium was set up with one black tetrahedron as in "A" of experiment 1 but with a small *Strombus* shell in place of "B." This



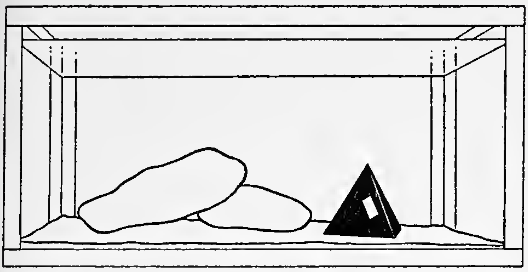

Text-fig. 3. Second arrangement of tetrahedrons in experiment 1.

was maintained for four days and neither fish paid the slightest attention to the tetrahedron. The dominant fish occupied the shell and the other rested in aquarium corners.

Experiment 3. One black tetrahedron was placed in another aquarium with two pieces of beach rock disposed so that one leaned on the other as indicated in Text-fig. 4. In this aquarium on August 12 were placed two *Pomacentrus*, two *Bathygobius* and four small *Sparisoma* sp. One *Bathygobius* immediately "inspected" the tetrahedron but did not enter. A few minutes later a *Pomacentrus* did the same. By three-quarters of an hour it was occupied by a *Bathygobius* which sat in the entrance with the head out as shown in Plate I, Fig. 3. The following day the same condition prevailed but when the goby was out of the tetrahedron it was visited by several of the scarids. One finally prevented the others from entering but the goby repossessed the place in a short time. On the fourth day the tetrahedron was turned as in Text-fig. 5. The goby which had been occupying it did not immediately find the entrance but clung with its ventral sucker to the place where the entrance had formerly been located. In



Text-fig. 4. First arrangement of tetrahedron in experiment 3.



TEXT-FIG. 5. Second arrangement of tetrahedron in experiment 3.

about one-half hour the new location of the entrance was located and the goby balanced itself on the cardboard edge with its head out. The other fishes had to content themselves with finding shelter under the beach rock. As with the other experiments this tetrahedron was not used after dark, but on one occasion the *Bathygobius* entered it after a flashlight was played on the aquarium for some time. This experiment was discontinued after five days.

Experiment 4. One black and one white tetrahedron were placed in an aquarium on August 17 as in experiment 1 but with both openings as in the start of experiment 3. Two new small *Pomacentrus* were placed in the aquarium. Neither shelter was seen to be entered until the third day, when one fish dominated the entire situation and entered both freely, but "lived" in the white one. The behavior was otherwise very like experiment 1. The other fish was completely subjugated and both spent the night out of the tetrahedrons. This experiment was terminated on the fifth day.

As far as these preliminary experiments go they tend to indicate that such forms of cardboard are acceptable, but not for use at night, that the entrances are memorized as to location, that light-colored retreats are preferred over dark and that all cavities within the area of one fish's domination are defended. Because of the refusal to accept the cardboard tetrahedrons at night, similar ones were constructed of concrete of identical external dimensions but slightly smaller inside because of the necessary thickness of the walls which were about one-quarter inch. Using these, the following series of experiments was undertaken.

Experiment 5. Two concrete tetrahedrons, painted white, were arranged essentially as in Text-fig. 2 but with both openings at the bottom. On January 2 at 3:00 p.m. two newly caught *Bathygobius* as nearly identical as possible were introduced. By 4:00 p.m. one had become dominant and was occupying the right-hand shelter. In another hour it occupied both alternately and the subjected individual remained in a corner of the aquarium. The next day each fish occupied a shelter, where they remained most of the time. There was no evidence of quarreling. There seemed to be no peck order. This behavior continued unchanged and on January 16 an empty conch shell was placed midway between the two shelters. There was immediate investigation by both fish but no entry into the shell was observed, as shown in Plate II, Fig. 1. No further changes were made in this aquarium and the fishes spent less and less time in the shelters so that by March 24 the doorways had become so overgrown with a filamentous algae as to completely block entry. If the fishes had forced their way through it when not observed, evidence of their entry would have been noticeable. Also by this time the fish had become so tame that if one placed a finger in the tank they would come to the surface and bite it. On March 27 one goby was in the "dominant" color phase and was mildly chasing the other. The difference in pattern has been discussed by Breder (1949) and illustrated in Plate II, Fig. 1.

Experiment 6. On January 3 an experiment was established identical with experiment 5 but with different individuals. The same day these fish established a peaceful relationship, each occupying a shelter as shown in Plate II, Fig. 2. The fish disappeared the next day, evidently having jumped out of the tank.

Experiment 7. The physical arrangements were as in experiments 5 and 6 but with one small *Pomacentrus leucostictus* and one small *P. adustus* Troschel as near the same size as possible. These were introduced at 6:00 p.m., January 3. There was no immediate entry but by nightfall one fish was found in each shelter. The next day it was apparent that the *P. leucostictus* was dominant over the other fish as was evidenced by the chasing, although both were in "possession" of their separate shelters. On January 11 an additional shelter was placed between the two tetrahedrons. It consisted of two small slabs of concrete standing on edge in the sand and a top of a similar slab on its side. Investigation by both fish was prompt and thorough. The conditions were unchanged by January 16 and there was little chasing or molestation. After an absence from the laboratory it was found on March 24 that only the *P. leucostictus* was present and it used the concrete slabs for shelter. On March 27 it used the shelter formerly occupied by the other fish.

Experiment 8. An aquarium was provided with one white tetrahedron and one conch shell. On January 3, two similar *Bathygobius* of about 70 mm. were introduced. Both shell and shelter were frequented the next day by what was evidently the dominant fish. The shelter was used first. Two small *Pomacentrus leucostictus* of about 10 mm. were added. Both gobies immediately chased them about and prevented entry into shell or shelter. The next day one *Pomacentrus* was dead. The other now occupied the shelter while its former occupant hid in a corner. It is to be noted that in both species the tetrahedron was used first. The next day at 8:15 a.m. the goby was in the shelter while

the *Pomacentrus* was out foraging and evidently unconcerned about the goby. By 9:00 a.m. the *Pomacentrus* was back and the goby in the corner. Later in the day the goby was seen to enter the shelter while the *Pomacentrus* was foraging again and voluntarily to leave the shelter before the *Pomacentrus* returned. This continued until January 8 when the *Pomacentrus* disappeared. It could have been easily eaten by the goby. This goby now occupied the shell, while the subjugated one had excavated a place under the shell which it occupied. By noon the dominant was back in the shelter and the subjugated back in the shell. Conditions continued in this fashion at least until January 16. After an absence from the laboratory only one goby was found and it sought shelter under the shell, March 24, but on March 28 it was back in the concrete shelter.

Experiment 9. Here the arrangement consisted of a red and a green tetrahedron and two *Pomacentrus leucostictus* almost too large to pass through openings in shelters established on January 8. One fish used the red shelter and the other hid in a corner. The next day one fish was in each shelter, and at 9:00 p.m. on the following day one was found in the red and none in the green, with the situation reversed at 10:00 p.m. The subjugated fish, whose fins had been damaged, was removed to another aquarium. The remaining fish from then on was in and out of both shelters. On January 16 two more shelters were added, one white and one black. There was no entry of these new shelters; the fish alternated between the two already present as shown in Plate II, Fig. 3. By March 24 the fish had become very tame and was seen on occasion to go into the green shelter, which was just barely possible because of the growth of the fish in the intervening time. Colors of tetrahedrons had become much reduced because of a growth of algal scum.

Experiment 10. An aquarium was arranged as in experiments 5 and 6, that is, with two white tetrahedrons. One *Pomacentrus* was introduced on January 10. This was the subjugated fish from experiment 9. It used both shelters indifferently, up to January 16 when a conch shell was placed between the two shelters. The fish hid in one of the shelters for a long time. After interruption in the observations because of an absence from the laboratory it was found that the fish was using the shell for residence on March 24. This may have had to do with the size of the opening and growth of the fish. There was no interfering algal growth in this tank.

In all these experiments with the concrete shelters the *Pomancentrus* stayed inside all night, as they do with shells.

## Discussion.

The preceding experiments represent observations covering 421 tank days on the reactions of 26 individual fishes in respect to shelters and companions. The individual experiments ranged from 1 to 85 days in length with a mean length of 42.1 days. The details may be conveniently shown by the following tabulation.

| Experiments and Number | Length in Days: Minimum | Mean | Maximum |
|---|---|---|---|
| 4 with cardboard shelters | 4 | 4.75 | 5 |
| 6 with concrete shelters | 1 | 67.0 | 85 |
| Total of 10 | 1 | 42.1 | 85 |

| Species Involved | Numbers of Individuals Used: Cardboard | Concrete | Both |
|---|---|---|---|
| *Bathygobius soporator* | 2 | 6 | 8 |
| *Pomacentrus leucostictus* | 8 | 5 | 13 |
| *Pomacentrus adustus* | — | 1 | 1 |
| *Sparisoma* sp. | 4 | — | 4 |
| Totals | 14 | 12 | 26 |

Since the series of experiments with cardboard shelters was carried out in August and those with concrete in January to March, a difference in water temperature in the aquaria existed, as given below.

| Season of Operation | Water Temperature °C.: Minimum | Mean | Maximum |
|---|---|---|---|
| August 2-20 | 29.0 | 30.1+ | 31.5 |
| January 2 to March 28 | 20.0 | 24.2— | 27.0 |

With these data and various general considerations it is possible to arrive at certain preliminary conclusions that should be basic to further, more detailed study of the behavior of these fishes by more refined and analytical techniques.

It is evident from all of these experiments and other observations that a dominant fish takes over the whole tank area and volume, defending all manner of shelters and shells. The evidently less desirable corners of the aquarium may or may not be left to the subjugated fish. This is in agreement with the earlier studies using more individuals and a larger variety of species (Breder, 1948). Incidental observations on similar fishes which became established in larger concrete tanks measuring 6′ × 3′ × 2′ deep showed that under such conditions an individual of either species might establish a territory of about half the bottom area of such a tank, or approximately 9 square feet. Observations in tide pools show a somewhat similar area for fishes of comparable size while those on open sandy beaches have been observed to control an area of a radius not more than 2 feet, which is equivalent to an area of approximately 12.5 square feet. Adults of *Pomacentrus leucostictus* generally do not defend an area with a radius of much over 3 feet or an area of approximately 28 square feet.

Although it is not indicated in the preceding remarks, it was clear during the summer tests in the experimental aquaria, as well as in numerous others, that there was much more fighting and chasing at that time than during the winter tests. This difference is evidently related to the difference in temperature of the water, 30.1° versus 24.2°, as well as perhaps the very slightly longer daylight periods in summer at this latitude. Re-

productive tendencies may also have influenced the gobies but such influences could not be present in the *Pomacentrus*, as they were immature.

As is obvious from the most casual observations, these experiments confirm the fact that both species under discussion are acutely aware of the physical features of their environment. They both spend much time swimming around and nosing into crevices of any new object or one which has been turned around or otherwise disturbed. As was noted by Breder (1949), they also will not infrequently return an object to its original site if they are capable of moving it. *Bathygobius* generally perches itself on the new object after it has "inspected" it for a time, perhaps obtaining further sensory data through the pelvic sucker. *Pomacentrus* on the other hand seldom touches such objects. As is indicated by the results of experiments number 5, 7, 9 and 10, these fishes show a considerable reluctance to adopt a new shelter once they are well established in old ones.

*Pomacentrus* will spend the dark hours in a shell or a concrete shelter, but will not so use a cardboard one, seeking instead, if only such is present, a corner of the aquarium. This fact would seem to indicate that a solid and firm structure free from vibration or other movement is sought for passing the night. When vision is possible, as in the daytime, this requirement is evidently less important although, as indicated by experiment 2, a shell is chosen as against a cardboard shelter while, as shown by experiments 5, 7, 9 and 10, no such selection is evident between shell and concrete shelter. This is the more notable because surely none of the fishes used ever had any prior experience with a shelter even approximating the form of a tetrahedron. Similar observations could not be made on *Bathygobius* for they are found both in and out of shelters by day or night, apparently being nearly aperiodic in habits. In experiment 3, however, they seemed to prefer the shelter of a cardboard tetrahedron over the more open shelter of rounded rocks.

There is no evidence from any of the 10 experiments that could be used to indicate any clear color preference in either the cardboard or concrete shelters. Evidently if there is any, it is of an order of magnitude too small to be made evident by these means.

Long residence in an aquarium evidently makes for less use of the shelters. Such behavior was especially marked in experiment 5 where shelters were completely abandoned. After some two months the entrances of the shelters were completely b'ocked by a dense growth of filamentous algae. There is nothing especially notable about this except the completeness of its nature. Anyone who has had long experience with fishes in captivity knows that the behavior of long resident fishes is often strikingly different from that of newly introduced individuals even long after the initial shock period has passed.

That *Pomacentrus* small enough to be swallowed by larger *Bathygobius* may attain a dominant position is in keeping with observations on other fishes that have a pronounced territorial behavior. For example, this is especially notable among nesting male fresh-water centrarchids as was indicated by Breder (1936).

## Summary.


1. In the small areas of 2 square feet, provided by the aquaria employed, the dominant individual of both young *Pomacentrus leucostictus* and *Bathygobius soporator* defended all shelters and shells, leaving only the evidently less desirable aquarium corners for the subjugated individual and sometimes not even those. In nature an area of more than 12 square feet may be defended.

2. Once these species have become established, it evidently takes some time for them to recognize a change in the location of the entrance to a shelter, since they repeatedly go to the site of the original entrance.

3. Cardboard shelters, while used during the daytime, are not used at night by *Pomacentrus*, but nights are passed in similar concrete shelters. This is indeterminate for *Bathygobius* since its behavior is nearly aperiodic. Evidently the solidity and rigidity of concrete and shell as compared with cardboard is a factor in this differential behavior.

4. A shell is preferred to a cardboard shelter, but no such preference could be detected between a concrete shelter and a shell.

5. If there is any color preference for such shelters it is not evident from these experiments and is therefore presumably a factor of small or no consequence.

6. Long residence in an aquarium evidently makes for less use of shelters, leading to complete abandonment of their use in one case of two *Bathygobius*.

7. *Pomacentrus* small enough to be swallowed by *Bathygobius* may nevertheless establish dominance over the latter for a time at least.

8. When these species are well established in an aquarium and accustomed to certain shelters, they have always been seen to elaborately "inspect" any newly introduced shelter, although they may be very reluctant to use it.


## Literature Cited.


Breder, C. M., Jr.

1936. The reproductive habits of the North American sunfishes (Family Centrarchidae). *Zoologica*, 21 (1): 1-48.

1948. Observations on coloration in reference to behavior in tidepool and other marine shore fishes. *Bull. Amer. Mus. Nat. Hist.*, 92 (5): 281-312.

1949. On the relationship of social behavior to pigmentation in tropical shore fishes. *Ibid.*, 94 (2): 83-106.

Longley, W. H. and S. F. Hildebrand

1941. Svstematic catalogue of the fishes of Tortugas, Florida, with observations on color, habits and local distribution. *Carnegie Inst. Washington Publ.* (535), *Papers Tortugas Lab.*, 34: i-xiii, 1-331.

## EXPLANATION OF THE PLATES.

PLATE I. Cardboard shelters.

FIG. 1. Experiment 1 showing dominant fish in right-hand shelter and the other in the background.

FIG. 2. Experiment 1 showing dominant fish in left-hand shelter after it had found the changed position of the opening; the other fish, not shown, is hiding in a corner.

FIG. 3. Experiment 3 showing dominant fish in entrance of shelter; others, not shown, are hidden under and behind rocks.

PLATE II. Concrete shelters.

FIG. 1. Experiment 5 showing both fish out of the shelters, the dominant (note pattern) perched on the newly introduced shell.

FIG. 2. Experiment 6 showing two fish each occupying a shelter.

FIG. 3. Experiment 9 showing the single fish occupying the green shelter. It is far back in the shelter, a condition made necessary by its large size. The red shelter is on the right and the black and white in the rear.

FIG. 1.

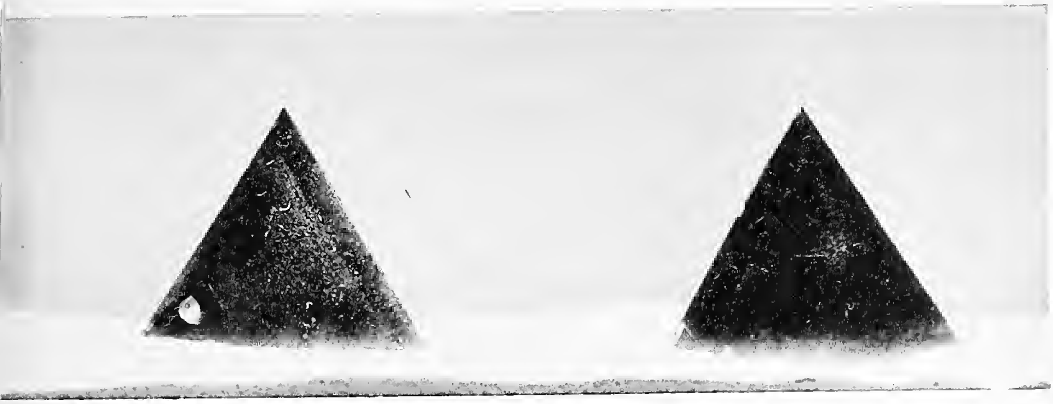


FIG. 2.

FIG. 3.

FACTORS INFLUENCING THE ESTABLISHMENT OF RESIDENCE
IN SHELLS BY TROPICAL SHORE FISHES.

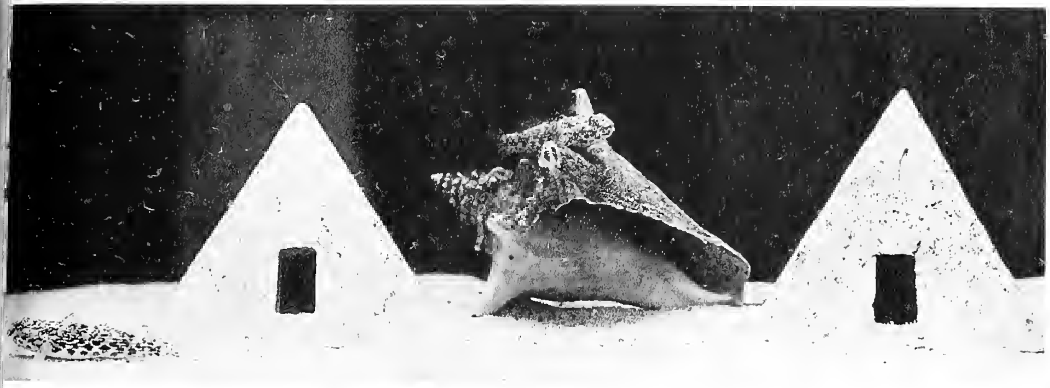


FIG. 1.

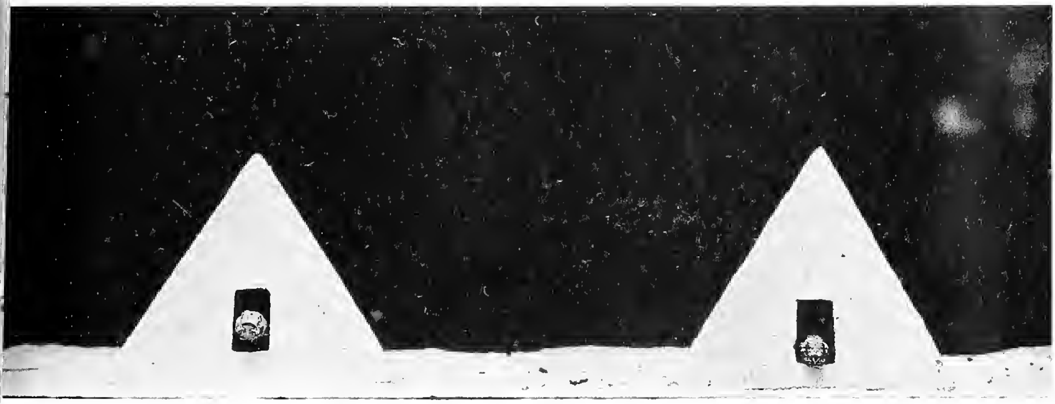


FIG. 2.

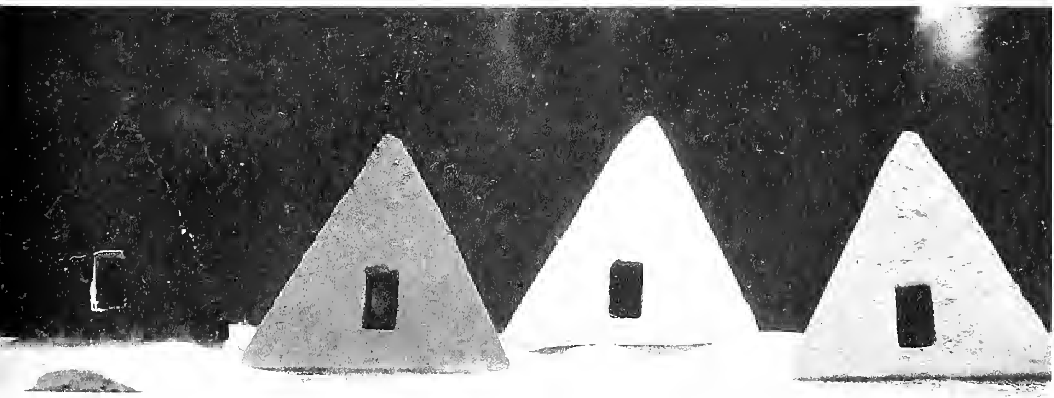


FIG. 3.

FACTORS INFLUENCING THE ESTABLISHMENT OF RESIDENCE
IN SHELLS BY TROPICAL SHORE FISHES.

# 13.

# Notes on the Behavior and Morphology of Some West Indian Plectognath Fishes.

EUGENIE CLARK.

*Department of Animal Behavior, The American Museum of Natural History.*

(Plates I & II; Text-figures 1-7).

A sizable fraction of the West Indian fish fauna comprises some 39 species of the Order Plectognathi. The deep sea triacanthids and the pelagic molids are infrequently reported, but the monacanthids, balistids, ostraciids, diodontids, tetraodontids and canthigasters are abundant in the bays and around the reefs, where they can be observed in their natural habitat and readily collected. During August and September of 1948 and February and March of 1949, the author had the opportunity of using the facilities of the Lerner Marine Laboratory of the American Museum of Natural History at Bimini, Bahama Islands, B.W.I., in making a study of the plectognaths of the area. The fish were obtained by dredging, seining, setting traps, hook and line fishing, and by dip-net fishing in floating *Sargassum*. Also, a number of young and larval forms were collected in plankton nets. Many of the fish were kept alive in large outdoor pens, concrete tanks and indoor aquaria where their behavior could be observed.

The author is indebted to Dr. Charles M. Breder Jr., Director of the Lerner Marine Laboratory, for many helpful suggestions.

### ***Balistes vetula*** Linnaeus.

More than 100 adults were maintained in the outdoor pens and concrete tanks at the laboratory. Most of these fish had been caught by hook and line and in traps. In the large outdoor pens, usually one or more of these fish were noticed resting on their sides on the sandy bottom. One might maintain this pose for as long as a minute and then suddenly right itself and swim off, apparently in good condition. At night many of these fish, which apparently were normal and healthy, were seen resting or "sleeping" in a vertical or nearly vertical position against a side wall or in a corner of their container, or lying flat on their sides on the bottom. Fish kept in smaller concrete tanks readily roll onto their side if an object is waved over the surface of the water, which apparently facilitates a better view for the observed as well as the observer.

### ***Melichthys piceus*** (Poey).

This species is common around the reefs south of Bimini and is easily recognized by the light blue lines at the base of the second dorsal and anal fins and near the posterior margin of the caudal fin, these lines standing out against the otherwise dark body and fins. More than sixty adults caught in traps and on hook and line were kept in the laboratory's live collection. While swimming undisturbed, the body is usually a blue-black color, but when the fish are handled out of water this changes to a dark green with some orange on the sides of the head.

At night, like *B. vetula* many of these fish rest against the sides and bottom of their container in nearly vertical positions.

### ***Monacanthus ciliatus*** (Mitchill).

This species was obtained in large numbers by dredging through *Thalassia* in the shallow water off the laboratory dock. Thirteen young specimens ranging from 14 to 28 mm. were collected in *Sargassum*. At these stages *M. ciliatus* is difficult to distinguish from *Stephanolepis hispidus* (Linnaeus). However, no adults of *S. hispidus* were collected and the occurrence of *S. hispidus* in this area is questionable. It is probable that these young are all *M. ciliatus*. One 28 mm. young showed a slight enlargment of scales on the caudal peduncle. The others, 14 to 24 mm., showed no sign of this scale modification. In late August several of these young fish were kept alive and at night showed locomotor disorganization in response to light described by Breder & Harris (see Breder, 1942).

Sexual dimorphism has been reported in several species of plectognath fishes (Fraser-Brunner, 1940a, 1940b). In *M. ciliatus* there is a marked sexual difference which has not been previously recognized. It is believed that the female has often been misidentified as a small *S. hispidus*, since these two species are separated in most keys (Jordan & Evermann, 1896-1900; Evermann & Marsh, 1902; Breder, 1929; Beebe & Tee-Van, 1933) by the size and shape of the ventral flap, a difference found between the sexes of *M. ciliatus* (Text-fig. 1) as will be seen in the following analysis of the sexual dimorphism in this species.

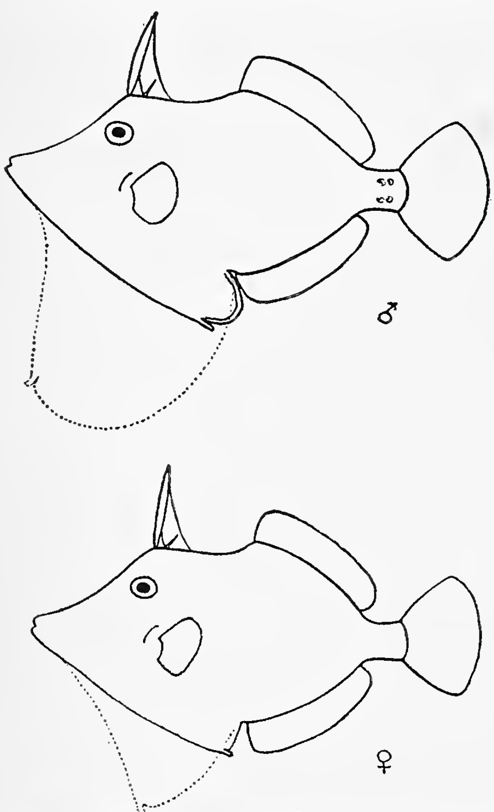
The sexes determined by examination of

78 adults (33 males and 45 females) were found to differ in the following respects:

1. The males have from three to eight (usually four) well-developed recurved spines on each side of the caudal peduncle. The females lack spines but in their place have enlarged scales which sometimes bear a small straight spinule. *S. hispidus* does not have this scale modification on the caudal peduncle in either sex.

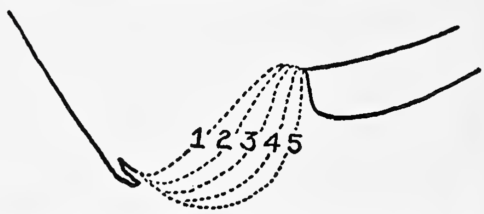
2. The males have a clear, dark, fine line near the margin of the ventral flap which is completely lacking in the females and immature fish. Specimens preserved in formalin retain this line.

3. The spread of the male ventral flap is on the whole much greater than that of the female. The spread was measured from the tip of the pelvic spine to the anus while the ventral flap was pulled out to its maximum. This length divided by the length of the snout (measured from the anterior margin of the eye to the opening of the mouth) gave values ranging from 1.3 to 2.6 with an average of 1.8 for the males and a range of 0.9 tc 1.7 with an average of 1.2 for the females. These measurements were taken on specimens preserved in 10% formalin for less than two hours and are slightly lower than for living material. More than 100 specimens of *S. hispidus* examined in the fish collection of the American Museum of Natural History, taken from other parts of the West Indies and Florida and ranging from 45 to 202 mm., gave comparative values from 0.5 to 0.9 (averaging 0.6). In many cases the flaps of these long-time preserved specimens were tightly folded and could not be pulled out. In some of the larger fish the flap spread might easily be equal to the length of the snout although in no case did the flap margin extend beyond the ventral spine as in types 2, 3, 4, and 5 in Text-fig. 2.




TEXT-FIG. 1. Diagrammatic sketches of a male and female *Monacanthus ciliatus* showing sexual dimorphism. The dotted lines indicate the extent of the ventral flap when fully spread.

4. The margin of the ventral flap in the males is a bright golden yellow whereas in the females it is a dull, pale, greenish-yellow.




TEXT-FIG. 2. Diagram of the expansible ventral flap of *Monacanthus ciliatus* with dotted lines showing five arbitrary posterior margins (see text).

5. In the males, the ventral flap extends more posteriorly to the pelvic spine than it does in the females. Text-fig. 2 shows a diagram of a semi-expanded ventral flap with five arbitrary margins indicated by the numbers one to five according to the degree of posterior extension. In types 3, 4, and 5, the anus is well inside a "pseudocloaca" as described for *Triodon* (Breder & Clark, 1947), though not quite as pronounced.

The specimens were all classified as closely as possible under these five types of ventral flap margins. The average male had a type 4 margin and the average female a type 2. The percentage of males and females falling into these artificial groups are as follows:

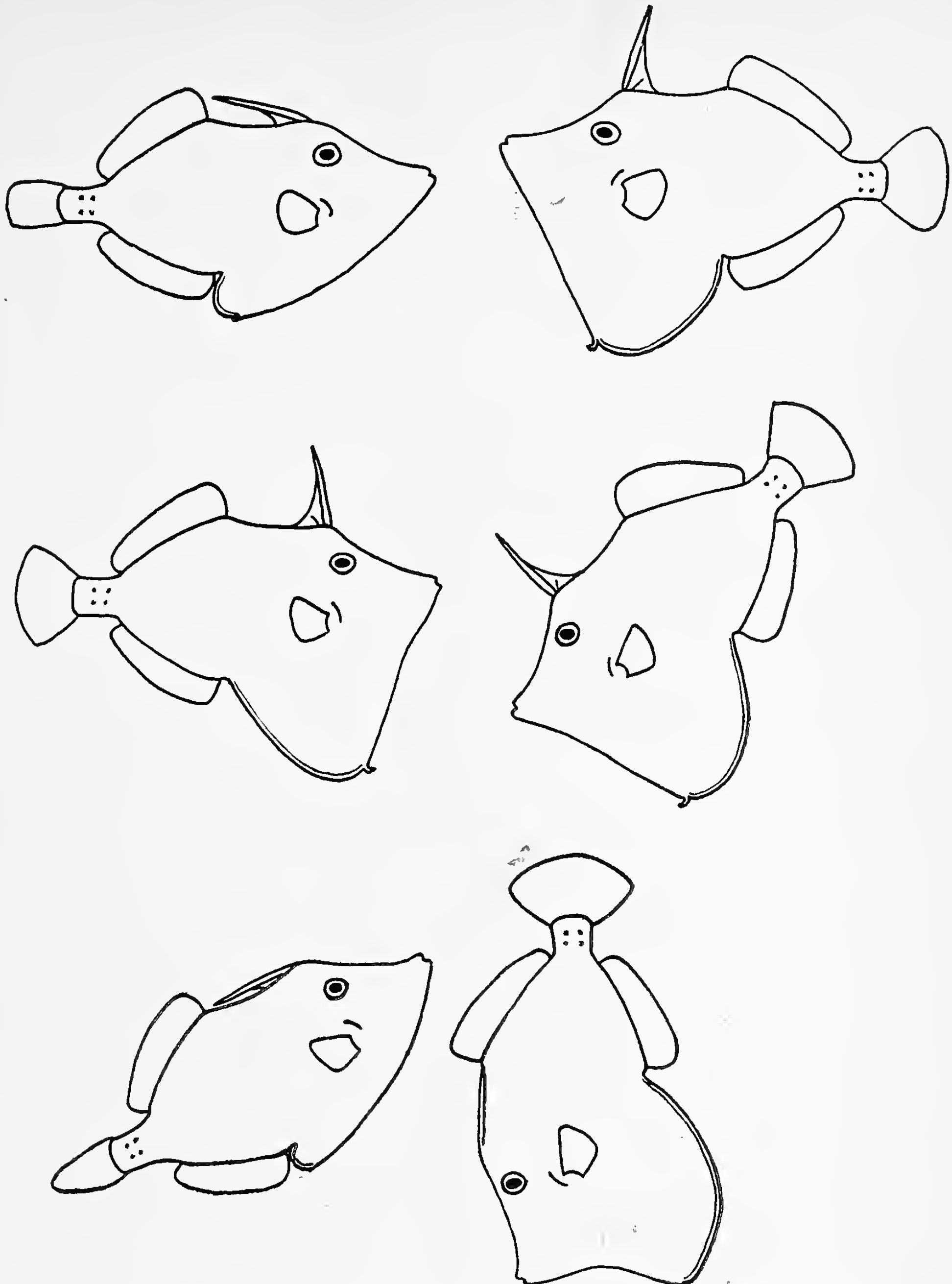
| Type of flap margin | 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|---|
| Percentage of males | 0 | 0 | 15.2 | 51.4 | 33.4 |
| Percentage of females | 35.6 | 46.6 | 17.8 | 0 | 0 |

The large percentage of females with a type 1 flap shows that the extension of the flap beyond the ventral spine is not a reliable character to separate this species from *S. hispidus*.[1]

6. The males on the average are larger than the females. The average standard length of the males was 64.5 mm., ranging from 58 to 76 mm., and for the females was 55.7, ranging from 43 to 71 mm.

Several isolated individuals, male and female pairs, and five groupings of four fish each, varying in sexual make-up, were kept in 15-gallon aquaria and their behavior was followed daily for a period of several weeks during August and September. A linear hier-

[1] The scale difference between *Monacanthus* and *Stephanolepis* (Fraser-Brunner, 1941), is a more reliable character for identification purposes.



TEXT-FIG. 3. Top to bottom illustrates three stages in an encounter between two males of *Monacantus ciliatus*. The dominant fish is shown on the right. Note the changes in the first dorsal and caudal fins, the ventral flap, and the angle of the long axis of the body. Due to the oval pupil, the gyroscopic action of the eyeball can be easily seen as the dominant fish goes into the "head stand" position.

archical order was usually noticeable in homosexual groupings and among the more numerous sex in heterosexual groups (i.e., one male and three females or three males and one female), but was not evident when equal numbers of each sex were present.

The dominant-subordinate relationship in these fishes is evident from several of their behavior patterns. The one most frequently observed is the sudden dashing of one fish at another. The subordinate fish swims away quickly, or may retreat to a corner, or turn over on its side and lie down on the bottom of the aquarium. The last two responses are given mostly by fishes low in an established hierarchical system. This aggressive behav-

ior appears to be the same as that noted in the "drive-order" of sunfish (Greenberg, 1947). Sometimes the dominant fish actually makes a sharp "nip" or peck at another fish —a common behavior used as a dominance criterion in studying fish hierarchies (Braddock, 1945, 1949; Breder, 1948). Occasionally these fish are seen nibbling at each other, especially at the opposite sex, but this gentle act, distinct from the sharp nip, does not appear to be part of the aggressive behavior indicative of the "nip-order."

The most violent aggressive behavior is a "tail slap." With a fast snap-like movement of the body, the dominant fish, after chasing and closely sidling its subordinate, flips its caudal peduncle (which in the male is armed with spines) at the other fish. Tail slapping has been observed in cichlid fishes (Noble & Curtis, 1939; Aronson, 1949) as part of a courtship pattern.

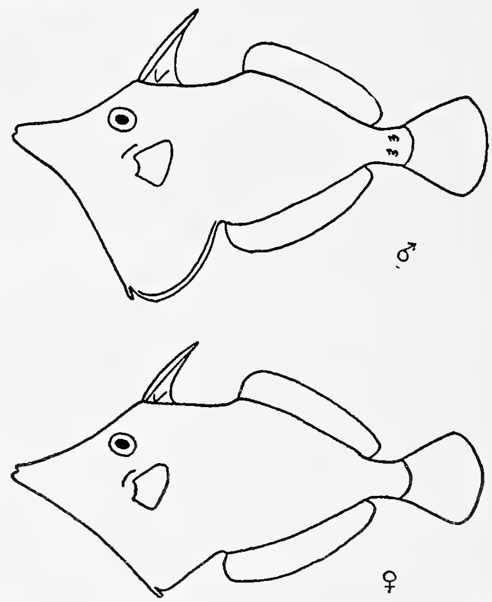
A rather spectacular behavior exhibited by *M. ciliatus* (especially males) involves the expansible ventral flap. The fish "noses down" until the long axis of the body is in a vertical position and the pelvic bone is swung forward until the flap behind it is fully expanded. The whole body appears stretched and tensed and quivering movements may accompany this posture. The caudal fin is expanded, but the dorsal spine is usually folded down against the back while the jointed pelvic spine may be either bent outward at a 90° angle or remain flush with the pelvic bone. This behavior occurs most frequently between members of the same sex and is usually started by the dominant fish (Text-fig. 3). During this act a noticeable color change takes place in the males. The body takes on more of a yellow color, especially the dorsal, anal and caudal fins, snout and ventral flap.

Monacanthids are occasionally observed standing on their heads in a vertical position (Longley & Hildebrand, 1941), in some cases with their noses on the ground, closely resembling an aquatic plant (Beebe, 1928; Breder, 1949). *M. ciliatus* frequently assumes a head-stand position when feeding from the bottom of an aquarium or when resting at night. It is also not uncommon for them to expand and then refold the ventral flap while swimming about apparently undisturbed even when no other fish are present. The combination of the head-stand position with the ventral flap expansion in the characteristic manner described above, however, is quite definitely associated with social behavior. Males sometimes behave in this manner before a female but more often the behavior was observed as part of an intrasexual aggressive pattern which included nipping and tail slapping.

In each group with an established "nip-order," the *omega* fish usually remained practically motionless in a corner or lay on its side on the bottom of the tank. The fins eventually became badly frayed and in two instances the fish died, undoubtedly as a result of the frequent attacks of the other fish. The *omega* fish was palest in color, almost white, whereas the most dominant fish stood out as the darkest in each group, its body being mostly a deep greenish-brown. This correlation between darkness of coloration and dominance has been noted intra- and inter-specifically in other fishes (Greenberg, 1947; Breder, 1948).

**Monacanthus tuckerii** Bean.

Four adults (3 males and 1 female), ranging from 39 to 60 mm., and nine immature specimens, ranging from 17 to 30 mm., were collected by dredging through *Thalassia* in shallow water off the laboratory dock and by dip net fishing in Sargasso weed. As in *M. ciliatus* the caudal spines, ventral flap size, color and marginal stripe indicate sexual dimorphism in the four adults examined (see Text-fig. 4). Data on this material are listed in Table I.




TEXT-FIG. 4. Diagrammatic sketches of a male and female *Monacanthus tuckerii* showing sexual dimorphism.

The pectoral fin ray count was 11 for all specimens except the two larger males, for which it was 12. The caudal fin ray count for all was 12.

The color of the males was a variable brown but usually with the upper half of the body darker than the lower parts. Usually a dark brown stripe along mid-side extended from just behind the gill opening on to the caudal fin. The whole body was covered with a light network of irregular lines. A sharp white line running along the mid-dorsal line extended from the mouth to the tail and was slightly broader between the eyes. The margin of the flap (unlike that of the female) is a golden yellow with a fine blue line near the edge. Scattered brown spots and suggestions of irregular vertical bands show up in the darker color phases.

TABLE I.

Measurements and External Sex Characters of *Monacanthus tuckerii.*

| Sex | *Standard length (mm.)* | *Dorsal fin count* | *Anal fin count* | *Caudal spines* | *Marginal stripe on flap* | *Ratio of flap spread to length of snout* |
|---|---|---|---|---|---|---|
| ♂ | 60 | II-36 | 35 | well devel. | present | 1.3 |
| ♂ | 59 | 34 | 35 | well devel. | present | 1.4 |
| ♂ | 39 | 33 | 33 | small | present | 1.3 |
| ♀ | 45 | 34 | 34 | absent | absent | 0.8 |
| — | 30 | 33 | 33 | absent | absent | 0.9 |
| — | 30 | 34 | 33 | absent | absent | 0.7 |
| — | 28 | 34 | 33 | absent | absent | 0.8 |
| — | 24 | 36 | 36 | absent | absent | 0.7 |
| — | 23 | 35 | 34 | absent | absent | 0.8 |
| — | 22 | 34 | 34 | absent | absent | 0.7 |
| — | 21 | 34 | 34 | absent | absent | 0.7 |
| — | 20 | 33 | 33 | absent | absent | 0.5 |
| — | 17 | 35 | 34 | absent | absent | 0.3 |

As in *M. ciliatus,* in late August some of the immature fish of this species (20 to 24 mm.) showed locomotor disorganization in response to sudden light.

**Cantherines pullus** (Ranzani).

Two immature specimens were collected in floating *Sargassum* and eleven adults were caught in traps near the laboratory dock. Data on these specimens—plus one museum specimen collected in Bimini on July 19, 1937 (AMNH No. 15164), indicated with an asterisk—are given in Table II to show the variation in fin count and the tendency to larger size of the males.

TABLE II.

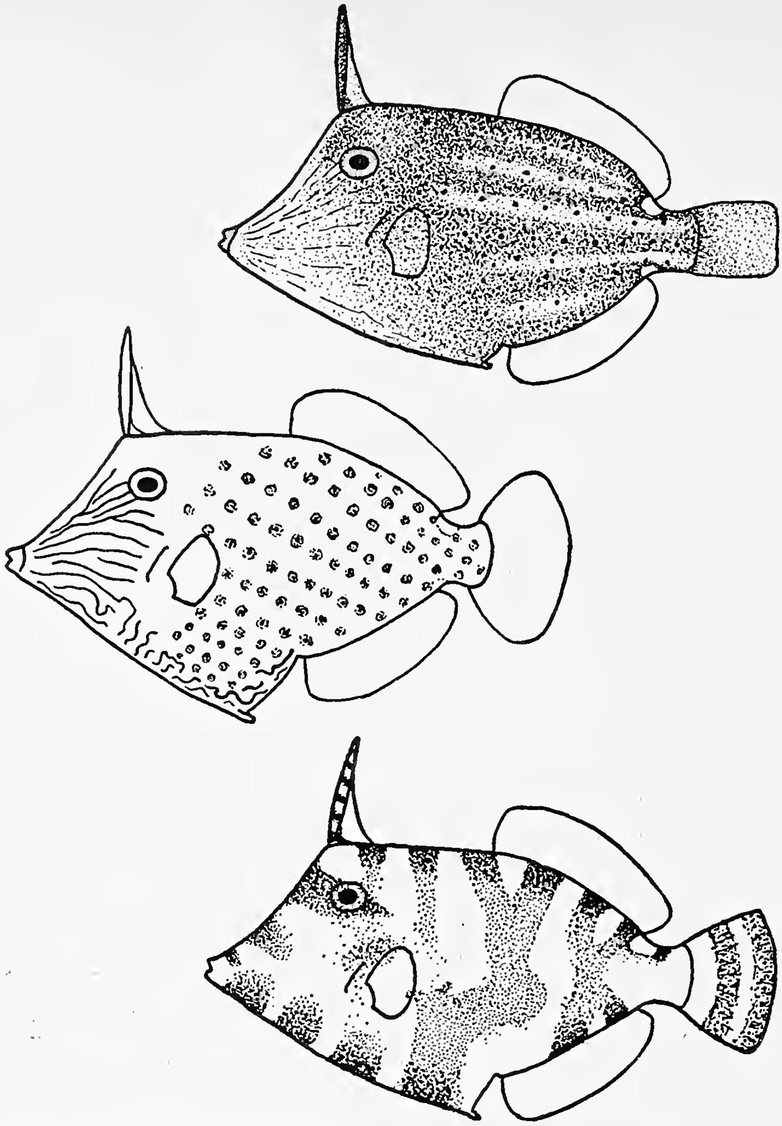
Measurements of *Cantherines pullus.*

| *Standard length (mm.)* | Sex | *Dorsal fin count* | *Anal fin count* | *Pectoral fin count* |
|---|---|---|---|---|
| 32 | — | II-34 | 30 | 13 |
| 38 | — | 35 | 32 | 13 |
| 111 | ♀ | 34 | 31 | 13 |
| 113 | ♀ | 34 | 30 | 13 |
| 116 | ♂ | 34 | 31 | 13 |
| 124 | ♂ | 34 | 30 | 13 |
| 125 | ♀ | 34 | 32 | 13 |
| 131 | ♂ | 36 | 31 | 13 |
| 132 | ♀ | 35 | 31 | 13 |
| 134 | ♂ | 34 | 30 | 13 |
| 137 | ♂ | 37 | 33 | 13 |
| 140 | ♂ | 35 | 31 | 14 |
| 143 | ♂ | 34 | 30 | 15 |
| *148 | ♂ | 36 | 31 | 13 |

Spines are not present on the caudal peduncle of any of these specimens. The young have been considered as a separate species, *C. amphioxys* (Cope), by most taxonomists. Although several authors have suspected the relationship, only Longley (1933) has correctly placed them in synonomy.

All the specimens collected were kept alive and color notes were taken. The 32 mm. specimen was a uniform silvery color and never showed markings or color variations. The 38 mm. specimen, practically identical with the figures for *Pseudomonacanthus amphioxys* (Parr, 1930), had a golden metallic sheen, brightest on tail, which sometimes faded to a dull white. The color pattern of this specimen varied somewhat, but usually dark brown areas were present which formed four irregular horizontal stripes on the posterior two-thirds of the body, the lowest not extending onto the caudal peduncle and the middle two forking anteriorly. Each stripe contained a row of regularly spaced dark spots. The head was without markings. A white spot on the mid-dorsal line just posterior to the second dorsal fin and just above the uppermost horizontal stripe, a good "field mark" in the adults previously not noted in descriptions of *C. amphioxys,* was conspicuous most of the time in this young specimen. Except for slight fading, these markings remained essentially the same after five months in 10% formalin, save the white spot, which darkened.

The adult specimens show remarkable color pattern changes which appear to be correlated more with the psychological and physiological state of the fish than with its background. Three rather distinct color phases (although sometimes overlapping) will be described: the horizontally striped phase, the spotted phase and the vertically banded phase. The first of these was seen when the adults were observed swimming undisturbed in aquaria and in the ocean, adult specimens being watched in shallow water among rocks off southern Bimini. They showed a pattern of horizontal stripes on the posterior two-thirds of the body, consisting of five light greenish-yellow stripes on a dark brown background. Closer examination revealed a number of regularly spaced, small, dark spots in this area as in the 38 mm. specimen. The anterior half of the body varied from a light tan to dark brown with some dull yellow spots above and behind the eye and occasionally there were about a dozen yellow lines on each side of the face, radiating from the mouth. Several dull yellow, wavy lines occurred on the lower part of the ventral flap. The white spot behind the second dorsal fin was always conspicuous in this phase of color-pattern and in addition a white spot on the mid-ventral line just behind the anal fin was usually noticeable. The first dorsal spine was a solid dark brown and the membrane behind a greenish-yellow. The



TEXT-FIG. 5. Sketches showing three different color pattern phases of *Cantherines pullus* (see text).

caudal fin varied from a light brown overcast with a dull greenish-yellow to a pale brownish-yellow. The pectoral fins were colorless and the second dorsal and anal fins colorless except for some orange on the proximal part of the membranes between the rays. This horizontally striped pattern phase is shown in Text-fig. 5 (top).

The spotted phase was first observed in an aquarium containing two adults (later dissected and found to be a male and a female). The male occasionally was observed to swim alongside the female, then somewhat in front of her, turn slightly on his side and point his nose downward at about a 45° angle. At this time the first dorsal spine was erected and quivered back and forth, and the membrane of the first dorsal fin became a brilliant sea green. The caudal fin was spread and the ventral flap, not appreciably expansible, was extended to its maximum and became a bright peacock blue in color. The body retained some of the horizontally striped pattern previously described. These stripes, however, took on a purplish-blue hue and were overlaid with conspicuous orange spots. During close sidling the male sometimes nipped at the female, who then showed an instantaneous and trenchant color pattern change. The horizontal bands in some cases faded completely and on a much paler bluish background, vivid orange spots with small dark brown centers (corresponding to the arrangement of faint spotting seen in the striped phase) appeared over the posterior two-thirds of the body. The radiating facial lines and undulating lines on the ventral flap were more clearly delineated. Both male and female showed this spotted pattern phase when pulled out of water with a net, the male

in addition showing a bright blue color on the face between the yellow radiating lines. This color pattern phase (see Text-fig. 5—center) seemed to appear when the fish was highly excited, during fighting or what may have been courtship. The female in one case (113 mm.) contained bright green mature ova which were easily squeezed out by slight pressure on the abdomen. From all the other adult specimens, however, no eggs or sperm could be forced out and when dissected none had ripe gonads.

The third rather distinct color pattern was observed at night when a light was flashed on the resting fish (see Text-fig. 5—bottom) and was occasionally seen during the day when a fish was resting in a dark corner. At such times these fish appeared "off guard" and could be caught by hand, whereupon they quickly changed to the orange spotted phase. The color pattern of resting fish was a dark brown mottling on a tan background in some places forming vertical bands—two sharp bands on the tail, one connecting the eyes, one large irregular one on the middle of the body from a fork below the second dorsal fin onto the ventral flap, and another, forked above and below, connecting the posterior part of the base of the second dorsal fin with the base of the ventral fin. Six dark rings were regularly spaced on the first dorsal spine. The white spot behind the second dorsal fin, although obscured by lighter and more irregular color patterns, was nevertheless present in the spotted and vertically banded pattern phases.

On two occasions when these fish were chased with a net and cornered in a concrete tank having a sandy bottom, the fish lay on their sides and remained motionless when poked. Their color blanched except for small, irregular blotches and they so closely resembled the bottom of the tank that they could barely be detected. This blanching appeared to be a case of matching the background, since the typical fright reaction was a color change to the orange spotted phase already described. When placed in formalin, the body, tail and first dorsal fin became a uniform dark brown.

### *Alutera punctata*

Jordan & Evermann (Agassiz?).[2]

Three adults (196, 197, and 264 mm.) were caught in traps. The smallest was a female from which mature ova were released when slight pressure was applied to its sides. The pale green eggs were sticky and demersal. Six young (47.7 to 66.4 mm.)[3] were examined from a dredged collection made near the laboratory dock on October 27, 1948. The fin counts of these nine specimens were: D. 34-37, A. 36-40.

The pattern on the adults was usually that of large, dark patches forming six saddle marks across the back and blending to form a wide, irregularly oblique band and interrupted vertical bands on the sides. A number of round, black spots were usually present on the upper middle portion of the sides of the body. When the fish became frightened the dark patches faded and the spots became more numerous and covered a larger surface. A male was observed to "nose-down" before a female while strongly vibrating his first dorsal spine through an arc of about 100°, but no color change was noticed to take place at this time as in *C. pullus*.

### *Alutera scripta* (Osbeck).

Five adults (414-513 mm.) caught on hook and line were kept alive in the outdoor pens. When swimming undisturbed the base color of the body was a light greenish-yellow with bright blue to purple dashes and dots running in broken horizontal lines. Irregular dark patches around the outline of the body (side view) were sometimes barely conspicuous while at other times they extended into irregular vertical bands. The vertical bands, as in *C. pullus*, were most noticeable at night when the fish were resting. The dorsal, anal and pectoral fins varied from colorless to yellow with yellow-brown rays. When the fish were frightened, the dark patches faded and round, dark spots appeared somewhat regularly spaced over the body.

### *Spheroides spengleri* (Bloch).

Two specimens were dredged in shallow water near the laboratory dock, a 78 mm. female and a 130 mm. male. Both showed remarkable inflating powers. Dissection showed a well defined ring-like constriction separating the ventral expansible part of the stomach from the stomach proper, the same as the condition described for *Spheroides maculatus* (Breder & Clark, 1947).

### *Spheroides marmoratus* (Ranzani).

Eight adults, 123 to 198 mm. in standard length, were obtained from traps set in the bay during February. Four were males from which motile sperm was easily squeezed out and four were females with well developed ovaries containing immature ova. In all cases the left ovary was about one-third larger than the right. The stomach, as in *S. spengleri*, was divided by a ring-like constriction. The background color of these fish varied from a rather uniform dark greenish-brown to a sandy white with ruptive dark bands on the head and back. The pale reticulations over the body and the spotting on the lower sides barely showed in the lighter phases. The belly varied from white to bright yellow. Most of the time these fish remained resting on the bottom of their aquaria and when disturbed, burrowed into the sand by means of their pelvic bones in the manner described

---

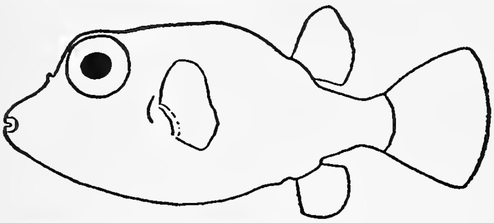
[2] The three adult specimens described here are certainly distinct from *A. schoepfi* (Walbaum) and appear to be the same as the *A. punctata* described in Jordan & Evermann (1896-1900). Longley (Longley & Hildebrand, 1941) however, has pointed out certain discrepancies in the literature regarding this species. The proper identity at present is uncertain.

[3] These are probably the young of *A. punctata* but are not distinguishable from those of *A. schoepfi* (Walbaum).

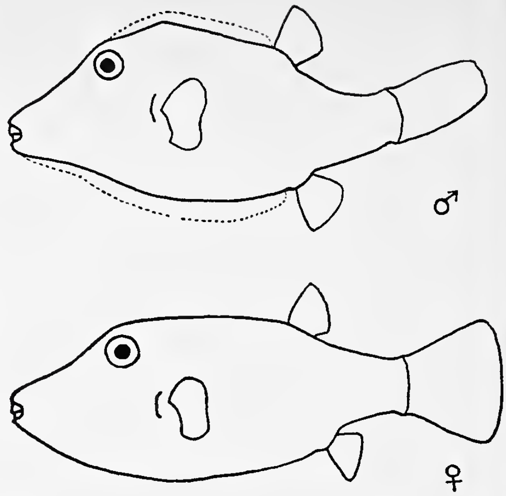
by Parr (1927) until only the top of the head and eyes were exposed.

**Canthigaster rostratus** (Bloch).

Three young specimens of 11, 13, and 16 mm. were caught by nets with floating *Sargassum.* When handled they showed a highly expansible belly region. An outline of the 16 mm. specimen, deflated, is shown in Text-fig. 6. Seven specimens (4.3 to 8.5 mm.) were found in plankton samples. Two adult females, 51 and 52 mm., and 21 adult males, 47 to 69 mm., were dredged near the laboratory dock. The males all showed an elevated point on the mid-dorsal line over the gill opening. The two females, like the young, lacked this character. Text-fig. 7 shows this difference in body form, which may be a secondary sex difference.



TEXT-FIG. 6. An outline sketch of a 16 mm. young *Canthigaster rostratus.*




TEXT-FIG. 7. Diagrammatic outlines of a male and female *Canthigaster rostratus.* The male is shown in the curved body position which it frequently assumes, especially when the mid-dorsal and mid-ventral ridges (indicated with dotted lines) are raised.

A number of adults were observed in aquaria, handled and "tickled," but unlike the younger specimens they could not be induced to puff out to the remarkable extent which is so characteristic of most gymnodonts. There is developed, however, a unique modification in the use of the expansible skin which apparently involves a mechanism quite different from that of puffing. When startled by a moving object or when placed together for the first time, the males were usually observed to raise the loose skin of their bodies, forming prominent mid-dorsal and mid-ventral ridges as indicated on Text-fig. 7 (top). Fish established in an aquarium for several days showed this behavior less frequently, although when a new individual was introduced this behavior was again observed, quite often among all the fish when approaching each other. During this "ridge lifting" the fish usually turns slightly onto one side and the tail is turned either downwards or more often upwards. Sometimes only the ventral ridge is pushed out. Occasionally an apparently undisturbed fish was seen swimming or resting in an angular position, with tail upwards, and a slight ventral ridge showing (see Pl. II, Fig. 6). Dissection showed the presence of a puffing mechanism the same as described for *Canthigaster cinctus* (Clark, 1949) but superficial examination showed no special anatomical modification to account for the peculiar ridge-lifting phenomenon.

Occasionally adult specimens were seen with an irregularly brown mottled pattern, dark to light brown areas on a pale background, and showed little coloring. More often, however, the following color pattern is seen: the upper part of the body is darker than the lower part and often a dark brown spot is evident just below the anterior base of the dorsal fin. The dorsal and ventral margins of the caudal fin are a dark brown. Sometimes two dark brown lines show on each side of the body, a more prominent upper line extending from above and behind the gill opening to the dorsal base of caudal fin and a shorter line starting some distance behind lower part of pectoral fin to ventral base of caudal fin. These two lines usually terminate in dark spots at base of caudal fin. There are radiating lines from the eye, which vary in number from four to nine and are limited to anterior, ventral and posterior part of rim of the eye, none crossing the mid-dorsal line of the head. These lines—and other lines and spots which vary considerably over the head, center and posterior parts of the body—are a purplish-blue. The base color on the side of the head is mainly a bright golden orange which fades to a dull olive yellow on the belly and lower sides of the body. The caudal and dorsal fin rays are bright orange. The pectoral and anal fins are colorless except for a pale orange yellow hue at their bases.

**Diodon hystrix** (Linnaeus).

Two young specimens of 44 and 140 mm. were caught in a dredge near the laboratory dock and one 62 mm. specimen was collected from floating *Sargassum* off southern Bimini. Four adults, 362 to 420 mm., were in the laboratory's live collection. In all the specimens the frontal spines were unmistakably shorter than the postpectorals and the caudal peduncle, dorsal and anal fins were not hidden when the fish were inflated. Adults were seen on several occasions when diving with goggles among coral heads off southern Bimini. They would lie very still in small crevices

until closely approached and then dart off to another hiding place.

***Chilomycterus antillarum*** Jordan & Rutler.

Three specimens, 108, 118, and 120 mm., were dredged near the laboratory dock. Hexagonal reticulations, coverings the dorsal and lateral regions of the body, were distinct in the various color changes of living specimens and also in fishes preserved in formalin.

### Other Plectognath Species.

Several other species collected at Bimini were examined from the live collection:

| | | |
|---|---|---|
| 6 *Balistes carolinensis* Gmelin | 17.1 | to 250 mm. |
| 6 *Canthidermis sufflamen* (Mitchill) | 362 | to 468 mm. |
| 14 *Rhinesomus bicaudalis* (Linnaeus) | 203 | to 320 mm. |
| 18 *Acanthostracion quadricornis* (Linnaeus) | 164 | to 276 mm. |
| 12 *Lactophrys trigonus* (Linnaeus) | 116 | to 338 mm.[4] |

### Summary.

Incidental notes on the behavior and/or morphology of *Balistes vetula, Melichthys piceus, Monacanthus ciliatus, M. tuckerii, Cantherines pullus, Alutera punctata, A. scripta, Spheroides spengleri, S. marmoratus, Canthigaster rostratus, Diodon hystrix* and *Chilomycterus antillarum* are reported. Detailed descriptions are included of the unusual head-standing aggressive behavior in *M. ciliatus*, the color changes of *C. pullus*, and the peculiar ridge-lifting phenomenon in *C. rostratus*. Sexual dimorphism in *M. ciliatus* and *M. tuckerii* is discussed along with problems concerned with the taxonomy of *M. ciliatus*.

### Bibliography.

Aronson, Lester R.

1949. An analysis of the reproductive behavior in the mouthbreeding cichlid fish, *Tilapia macrocephala* (Bleeker). *Zoologica*, 34 (3): 133-158.

Beebe, William

1928. Beneath Tropic Seas. New York: G. P. Putnam's Sons: 234 pp.

Beebe, William & Tee-Van, John

1933. Field Book of the Shore Fishes of Bermuda. New York: G. P. Putnam's Sons: 337 pp.

Braddock, J. C.

1945. Some aspects of dominance-subordination in the fish *Platypoecilus maculatus*. *Physiol. Zool.*, 18: 176-195.

1949. The effect of prior residence upon dominance in the fish *Platypoecilus maculatus*. *Physiol. Zool.*, 22 (2): 161-169.

[4] The writer examined two specimens of this species in which the carapace was completely fused behind the dorsal fin just anterior to the free scale on the caudal peduncle—an atypical character for this species.

Breder, C. M., Jr.

1929. Field Book of Marine Fishes of the Atlantic Coast from Labrador to Texas. New York: G. P. Putnam's Sons: 332 pp.

1942. On the phenomenon of locomotor disorganization induced by strong light in small plectognath fishes. *Copeia*, (4): 211-213.

1948. Observations on coloration in reference to behavior in tide-pool and other marine shore fishes. *Bull. Amer. Mus. Nat. Hist.*, 92 (5): 281-312.

1949. On the relationship of social behavior to pigmentation in tropical shore fishes. *Bull. Amer. Mus. Nat. Hist.*, 94 (2): 87-106.

Breder, C. M., Jr. & Clark, Eugenie

1947. A contribution to the visceral anatomy, development, and relationships of the plectognathi. *Bull. Amer. Mus. Nat. Hist.*, 88 (5): 287-320.

Clark, Eugenie

1949. Notes on some Hawaiian plectognath fishes, including a key to the species. *Amer. Mus. Novitates*, (1397): 1-22.

Evermann, B. W. & Marsh, M. C.

1902. The fishes of Porto Rico. *Bull. U. S. Fish Comm. for 1900;* 49-350.

Fraser-Brunner, A.

1940a. Notes on the plectognath fishes. IV. Sexual dimorphism in the family Ostraciontidae. *Ann. Mag. Nat. Hist.*, ser. 11, 6: 390-392.

1940b. The fishes of the genus *Pseudomonacanthus* with descriptions of two new species. *Bull. Raffles Mus.*, (16): 62-67.

1941. Notes on plectognath fishes. VI. A synopsis of the genera of the family Aluteridae, and descriptions of seven new species. *Ann. Mag. Nat. Hist.*, ser. 11, 8: 176-199.

Greenberg, B.

1947. Some relations between territory, social hierarchy, and leadership in the green sunfish (*Lepomis cyanellus*). *Physiol. Zool.*, 20 (3): 267-299.

Jordon, D. S. & Evermann, B. W.

1896-1900. Fishes of North and Middle America; a descriptive catalogue of the species of fish-like vertebrates found in the waters of North America, north of the isthmus of Panama. *Bull. U. S. Nat. Mus.*, 47.

Longley, W. H.

1933. Preparation of a monograph on the Tortugas fishes. *Carnegie Inst. Wash. Year Book*, (32): 293-295.

Longley, William H. & Hildebrand, Samuel F.

1941. Systematic catalogue of the fishes of Tortugas, Florida. *Carnegie Inst. Wash. Publ.*, (535): 331 pp.

Noble, G. K. & Curtis, B.

1939. The social behavior of the jewel fish, *Hemichromis bimaculatus* Gill. *Bull. Amer. Mus. Nat. Hist.*, 76 (1): 1-46.

PARR, A. E.

1927. On the functions and morphology of the post clavicular apparatus in *Spheroides* and *Chilomycterus*. *Zoologica*, 9: 245-269.

1930. Teleostean shore and shallow-water fishes from the Bahamas and Turks Island. *Bull. Bingham Oceanogr. Coll.*, 3 (4): 1-148.

## EXPLANATION OF THE PLATES.

### PLATE I.

FIG. 1. A male *Monacanthus ciliatus* with the ventral flap fully expanded.

FIG. 2. A male *Mocanathus ciliatus* in the "head stand" position.

FIG. 3. *Canthigaster rostratus.* Male on left exhibits prominant mid-dorsal and mid-ventral ridges.

### PLATE II.

FIG. 4. *Canthigaster rostratus.* Male on right shows mid-dorsal and mid-ventral ridges.

FIG. 5. *Canthigaster rostratus.* Front view of mid-ventral ridge.

FIG. 6. *Canthigaster rostratus.* Swimming slowly in the angular position described in text. The mid-ventral ridge shows slightly.

FIG. 1.

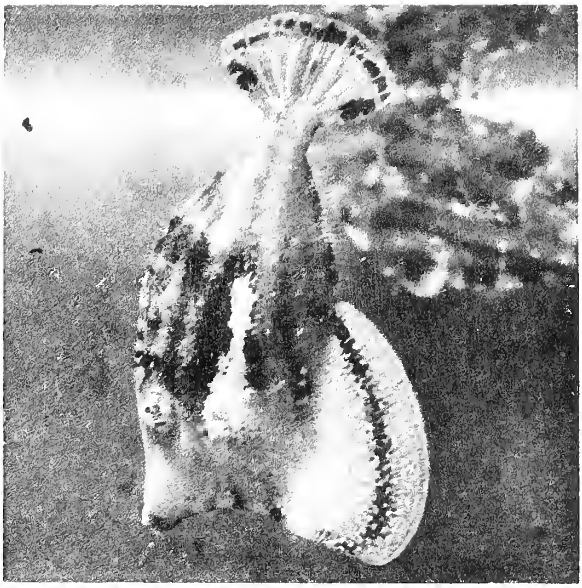


FIG. 2.

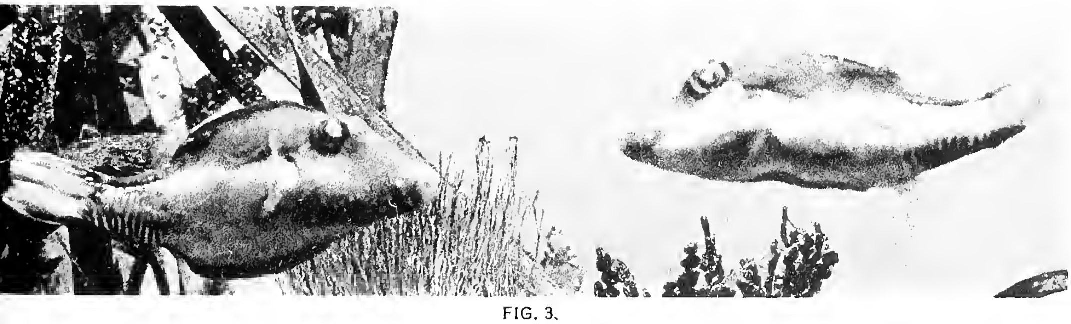


FIG. 3.

NOTES ON THE BEHAVIOR AND MORPHOLOGY IN SOME WEST INDIAN PLECTOGNATH FISHES.

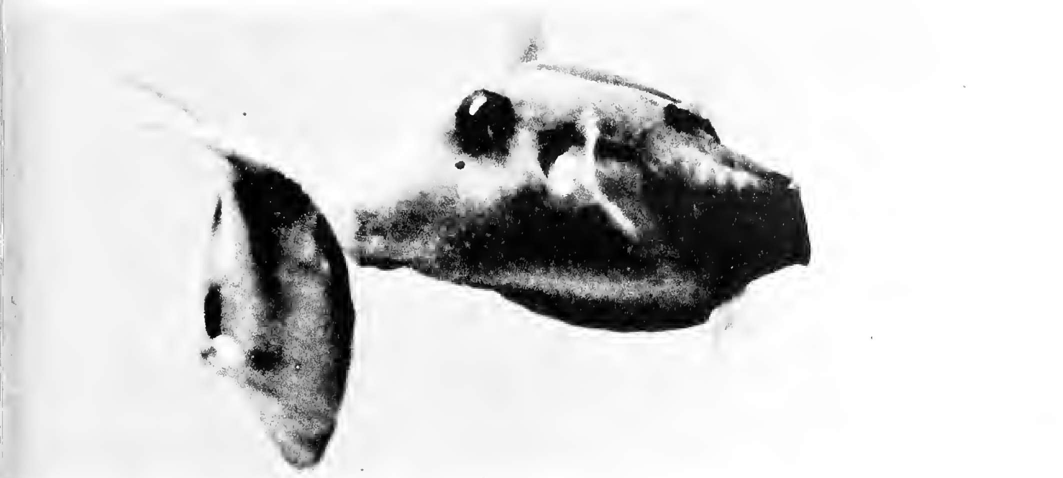


FIG. 4.

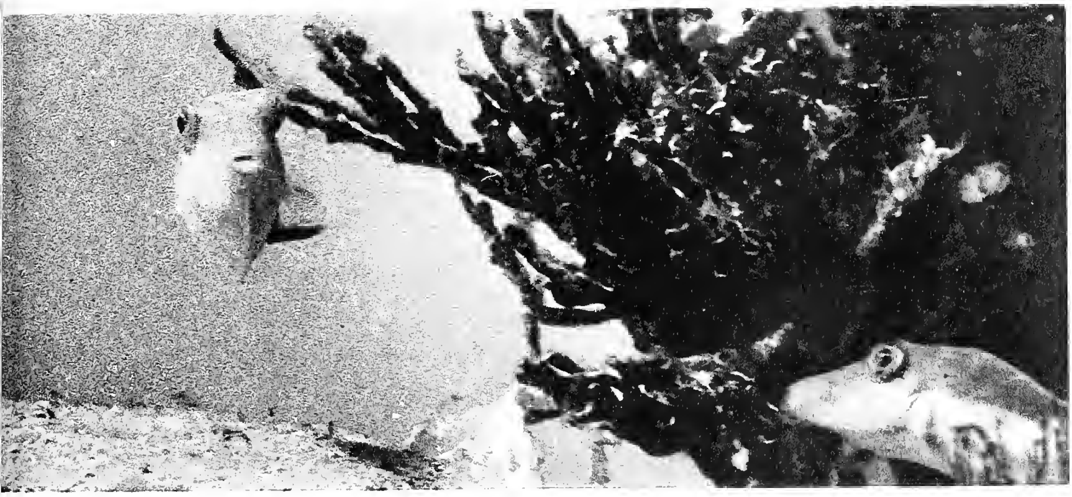


FIG. 5.

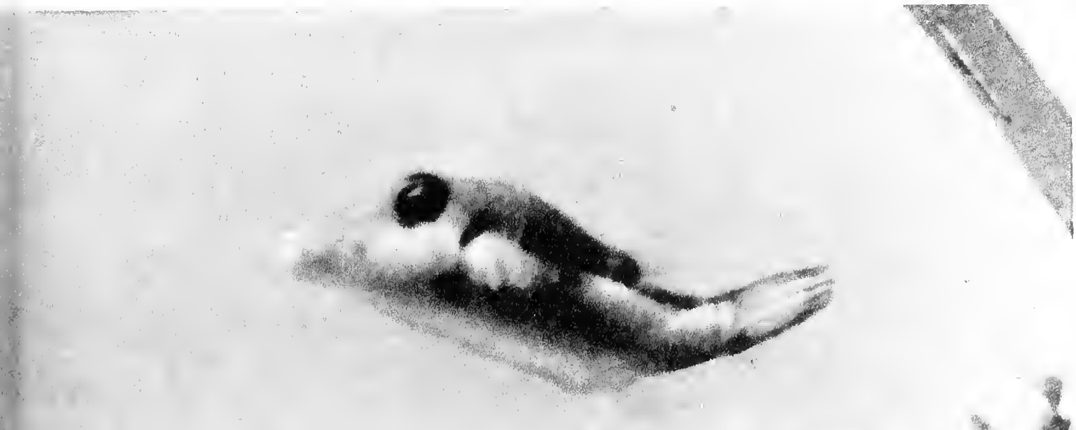


FIG. 6.

NOTES ON THE BEHAVIOR AND MORPHOLOGY IN SOME WEST INDIAN PLECTOGNATH FISHES.

# 14.

# The Effect of Alloxan on the Pancreas, Liver and Kidney of the Teleost, *Lebistes reticulatus,* with Notes on the Normal Pancreas.

LEONARD L. GROSSO.

*New York University*[1] *and The American Museum of Natural History.*

(Plates I-IV).

CONTENTS.



## INTRODUCTION.

In 1937 Jacobs reported that rabbits given an intravenous injection of alloxan suffered a hyperglycemia which is followed by a marked and often convulsive hypoglycemia. He alleviated the hypoglycemic state by glucose administration but made no histological studies of the pancreas. Dunn, Sheehan & McLetchie (1943), while studying the effects of a number of nephrotoxic drugs in rabbits, included the compound. They confirmed the pronounced blood sugar level changes and in addition reported extensive damage to the insulinogenic beta cells of the islands of Langerhans. Dunn & McLetchie (1943), using rats, continued the work and showed that the hypoglycemic state is temporary and is very soon followed by a permanent hyperglycemia. They considered the blood sugar level changes to be a physiological reflection of the demonstrated cytological alterations of the beta cells. That the effects are not due to an insulin inactivation by alloxan or to the alloxan per se, has been shown by Goldner & Gomori (1944a, 1944b), Kennedy & Lukens (1944), and Corkill *et al* (1944).

Following these reports, alloxan studies have been extended to include many different animals, among which are the following: dog (Goldner & Gomori, 1943; Houssay, Brignone & Mazzocco, 1946), cat (Ruben & Yardumian, 1946), sheep (Jarrett, 1946), monkey (Banerjee, 1944), pigeon (Goldner & Gomori, 1945), duck (Mirsky, 1945), turtle (Ramos, 1944), frog (Seiden, 1945), toad (Biasotti & Porto, 1945), elasmobranch and marine teleosts (Saviano, 1947a, 1947b). It has been found that all of these animals are affected in some degree by alloxan, and may show either histological or physiological changes, or both.

Following the administration of a diabetogenic dose of alloxan there occurs a characteristic tri-phasic blood sugar level curve. An initial rise in blood sugar at 2-4 hours after the drug administration, a secondary marked and often fatal hypoglycemia after 6-12 hours, finally a permanent hyperglycemia is noted (Duff & Starr, 1944; Houssay, Orias & Sara, 1945; Lazarow, 1946). That the curve may be tetra-phasic is indicated by the work of Shipley & Beyer (1947) who noted a slight initial drop in blood sugar level at 15-30 minutes after the alloxan administration.

In some mammals cytological changes in the beta cells have been reported to take place very rapidly. Hughes, Ware & Young (1944) claim that degranulation is detectable 5 minutes after a subcutaneous diabetogenic injection in the rat. In most animals studied, degranulation, nuclear pycnosis and cytolysis with an accompanying distortion of island architecture occurs within 24 hours. These changes, once established, are permanent.

It is claimed by some investigators that a number of complications and effects upon other organs accompany the diabetic state produced by the alloxan administration. Goldner & Gomori (1943), Kendall *et al* (1945) and Herbut *et al* (1946) report a fatty infiltration of the liver. Necrosis of this organ is recorded by Herbut *et al* (1946), Lazarow & Palay (1946), and Ruben & Yardumian (1946). Acute renal damage demonstrated histologically by vacuolation and desquammation of the convoluted tubules is reported by Dunn, Sheehan & McLetchie (1943), Bennett & Behrens (1946) and Jarrett (1946). Pancreatic acinar tissue injury is claimed by Di Pietro & Cardeza (1946) and Duff *et al* (1947). An extensive hemolysis is indicated by the work of Kennedy & Lukens (1944) and Gyorgy & Rose (1948). Although most investigators have found that the island damage is limited to the beta cells, there are reports that the island alpha cell type is also affected (Duff & Starr, 1944; Saviano, 1947).

In view of these findings, it became of interest to study the effects of alloxan upon

[1] Accepted in partial fulfillment of the requirements for the degree of Master of Science at New York University, June 1949.

the viscera of the teleost, *Lebistes reticulatus* Peters.

As a necessary preliminary to the alloxan study, the location and the cytology of the islet of Langerhans was determined. It has been known for many years that fishes possess the equivalent of the mammalian islands of Langerhans. It is usual for the islet tissue of a teleost to be condensed into a few, and sometimes into only one, nodule of a large size. The islets may in some species be so large that they are visible with the naked eye. Stannius in 1846 reported the presence of a variable number of bodies in the abdominal cavity of the bony fishes. He associated these with the lymphatic and circulatory systems, but from the description and location given it is now known that the structures are the islets of Langerhans. After Langerhans directed attention to cell aggregations in the pancreas of the rabbit in 1869, there were many attempts to find their homologue in other forms. Harris & Gow (1894), in a comparative study of the pancreas, neglected the fish pancreas because they doubted the existence of such a functional organ in the class. Laguesse in 1895 reported the presence of islet epithelial cells in the teleost *Crenilabrus melops* (Linnaeus). In the same year Diamare described in *Lophius piscatorius* Linnaeus a macroscopic nodule about the size of a pea. On histological grounds he considered it to be analogous (in a report 3 years later he used the term homologous) to the mammalian islands of Langerhans. In the same report he listed several smaller bodies having the same structure as the large body. The studies continued and in a few years it was shown that islet epithelial cells could be demonstrated, either macroscopically or microscopically, in a variety of species of both fresh water and marine teleosts.

That the islets of the teleosts are composed of different cell types was noted as early as 1898 by Massari. He reported that the nuclei of all the islet cells possess the same staining qualities, but that the cytoplasm of some of the cells is more chromophilic than in other islet cells. Jackson (1922), using the differential solubility method of Lane, concluded that the teleost islet consists essentially of alpha and beta cells. Bowie in 1924 demonstrated that the islet tissue of *Neomaenis griseus* (Linnaeus) consists of three types of granular cells; he termed these alpha, beta and gamma cells. In Bowie's report no mention was made of the presence or absence of the agranular "C" cell such as has been reported to be present in the guinea pig pancreas. In the present study it was thought that the use of the azan stain, which has been shown to be capable of demonstrating all islet cell types reported to exist, would yield some information on this important fundamental point. It was also expected that the alloxan study might supplement the cytological study of the normal islet.

The experimental work of this study was carried on in the laboratory of the Department of Fishes and Aquatic Biology of The American Museum of Natural History. The author expresses his appreciation to Dr. Charles M. Breder, Jr., and Miss Priscilla Rasquin for their valuable suggestions and criticisms of the manuscript. Thanks are due to Dr. Ross F. Nigrelli for his reading of the manuscript.

## Materials and Methods.

Mature, well-fed, healthy, active *Lebistes reticulatus* were selected for the experiment. Three series of experiments were established in an attempt to determine the effect of different dosages, and if possible ascertain the upper sub-lethal dose and the minimal dose capable of producing islet cell changes.

In the first series of experiments 14 females were kept immersed in a 0.05% alloxan solution. This concentration was lethal to some and deaths occurred as follows: 1 in the 0-10 hour interval, 2 in the 10-20 hour interval, 6 in the 20-30 hour interval. Two fish were sacrificed at the end of the first 10 and 20 hours. One, when found in a moribund condition at 40 hours, was sacrificed. Fourteen males were kept immersed in a 0.05% alloxan solution. Deaths were recorded as follows: 2 in the 0-10 hour interval, 2 in the 10-20 hour interval, 6 in the 20-30 hour interval. Two fish were killed at the end of the first 10 and 20 hours. All specimens were fixed in Bouin's fluid.

In the second series of experiments 14 females were kept immersed in a 0.025% alloxan solution. One death occurred; this was in the 30-44 hour interval. Two fish were sacrificed at 10, 20, 44 and 70 hours after the start of the experiment. Two were killed on the fifth and seventh days. All of these were fixed in Bouin's fluid. The one remaining fish was killed and fixed on the ninth day in Flemming's fluid. Fourteen males were kept immersed in a 0.025% alloxan solution. Two fish were killed at the 10, 20, 44 and 70 hour intervals. One fish was found dead at the 20 hour interval. Two fish were sacrificed on the fifth and seventh days. Bouin's fluid was used as a fixative for all of these. The last fish, for which Flemming's fluid served as the fixative, was sacrificed on the ninth day.

In the third series of experiments 14 females were kept immersed in a 0.013% alloxan solution. Two fish were killed after 10, 20, 44 and 70 hours. Two fish were sacrificed on the fifth and seventh days. Bouin's fluid served as the fixative for these. On the ninth day one fish was fixed with Flemming's fluid. The last fish was maintained until it died on the thirty-ninth day. Fourteen males received similar treatment. The last male died on the forty-first day.

The fish were kept in groups of seven in two-gallon aquaria, allowing 5 liters of solution for this number. Males were kept separate from the females. Tanks were maintained without plants or snails. Fresh alloxan solutions using conditioned water were made up semiweekly. For controls, mature, active

male and female fish of approximately the same size as the experimental animals were used. Both experimental and control fish were maintained on a diet consisting of approximately 12% protein, 2% fat and 32% carbohydrate. In addition, algae was available for the control fish; this growth was lacking in the experimental tanks. The temperature averaged 72°F., the high being 73°F., the low 69°F.

In preliminary tests for differentiating the various islet cells, Helly's, Zenker's, and Bouin's fluids were used as fixatives. It was found that Bouin-fixed tissue, washed in water, permitted a more highly specific coloration of the islet cells than tissue fixed in the other fluids tested. In the main part of this experiment, as has already been noted, Bouin's fluid was used exclusively, except in the four cases specified in which Flemming's fluid was used. The control fish were fixed in either Bouin's or Flemming's fluid. Fish to be fixed in Bouin's fluid were killed by placing them in the fixative; those to be Flemming-fixed were killed by cutting the spinal cord. The viscera were immediately removed and placed in the respective fluid. Tissue was left in Bouin's fluid for 8-10 hours, in Flemming's fluid for 24 hours, washed in water, passed through graded alcohols, xylol, and embedded in paraffin. Sections were cut at 4 and 5 microns. One of the two fish sacrificed at each time interval in each of the series, was stained by the Gomori modification of the azan stain; the other was stained with Harris' hematoxylin counterstained with eosin. Thus for every time interval (excepting the ninth day) in each series, one female and one male were stained with hematoxylin-eosin, one female and one male were stained with the azan stain. Harris' hematoxylin and eosin were used for the Flemming-fixed tissue. A number of the sections from fish killed at each time interval of each series were checked for the presence of hemosiderin with 2% potassium ferrocyanide and eosin.

To determine the position of the islet of Langerhans, serial sections were prepared. Fish were fixed using Bouin's fluid. To aid in penetration the abdominal wall was punctured so as to allow the fixative to flood the abdominal cavity quickly. Decalcification was accomplished by the phloroglucin-nitric acid method. The bodies were passed through graded alcohols, xylol, and embedded in paraffin. Cross, frontal and sagittal sections were cut at 5 microns. Staining was with Harris' hematoxylin and eosin.

## Normal Morphology of the Pancreas.

The exocrine pancreas of *Lebistes reticulatus* is a diffuse type with the cells arranged in bands. The greater part of these are found in the mesenteric area about the anterior part of the intestine and the spleen; often they extend posteriorly to the limit of the abdominal cavity. In addition, intrahepatic acinar cells are found in some specimens. The endocrine epithelial pancreatic cells are separate from the exocrine pancreas and form one compact nodule. As a rule this islet lies slightly anterior to the spleen; occasionally it is found extending to that organ, so that the two are seen in the same cross section. It is almost always situated in the mesentery on the left ventral surface of the stomach above the liver as seen in Figs. 1 and 3 (sometimes it is on the median line as in Fig. 2). It is in the area in which are located the mesenteric and hepatic arteries, the portal and splenic veins. The median margin of the structure is often seen to be in contact with the bile duct or the gall bladder. In cross section the islet is either oval or elliptical in shape; the former shape is more commonly found. In sagittal and frontal sections it appears elliptical. Owing to its pale pink color and thickness, it may be see macroscopically in large specimens as a pin point against the more translucent surrounding tissue.

The islet is bounded by a delicate fibrous connective tissue capsule. Occasionally a partial encirclement by the exocrine pancreatic cells is noted; this is seen in Fig. 7. Very delicate supporting connective tissue trabeculae are visible in some sections. No large blood vessel is seen to penetrate the islet; a very abundant blood supply is received through arterioles from the adjacent large blood vessels. Large conspicuous capillaries are abundant but are not equally distributed throughout the organ. Near the median border they are so numerous that in many cases they are separated from one another by two, and in some sections one, cell thickness only. In this region the capillaries are nearly parallel. Because of this arrangement the cells between them appear to be in columns or bands.

In routine hematoxylin-eosin preparations the pancreatic acinar cells stain very deeply. The zymogen granules are found in the inner zone of the cell, while the spherical nucleus with a centrally placed nucleolus is situated at the base of the cell. The islet cells are smaller and stain lighter than the exocrine pancreatic cells. That more than one type of cell is present in the islet is suggested by nuclear differences. Although there is a slight difference in chromaticity of the cytoplasm in different areas, cytoplasmic structural differences which could be used as criteria for cellular differentiation are not visible in the hematoxylin-eosin stained sections. The cells which stain darker are largely restricted to the marginal border and are usually arranged in bands between the capillaries that are so numerous in the area. Because of this arrangement these cells have a richer blood supply than other islet cells. Cell boundaries are not very distinct, but from the nuclear arrangement the cells appear to be cylindrical or spindle-shaped. The nuclei of these cells are oval, stain darkly and are filled with numerous minute chromatin granules. The nucleolus is distinct and centrally placed. The slightly lighter-stain-

ing cells are irregularly polyhedral in shape and are larger than the darker-staining elements. The nuclei are situated nearer to one end of the cell, are almost always round and are larger than the previously discussed nuclei. One or two eccentrically placed nucleoli are found. The darker-staining elements are the beta cells, the lighter elements are the alpha cells. A third type of cell is indicated and is present almost exclusively at the periphery of the organ. The cytoplasm takes very little stain, is very clear, and often is visible only with optimum staining conditions. The nucleus of this cell type is very large and except for a centrally placed nucleolus is also clear. This is the "D" type of cell.

The presence of these three types of cells was verified and further differences between them made evident when the azan stain was employed. With this stain the beta cell boundaries became more distinct and the fusiform shape indicated by the hematoxylin-eosin stain was confirmed. The cytoplasm when relatively degranulated is bluish and often a very small agranular area is seen at one side of the nucleus. The granules of this cell type are minute and stain reddish. As the number of granules increase and become crowded the cytoplasm itself seems red. The oval nucleus containing a distinct nucleolus stands out very clearly in the center of the cell. Because of this nuclear disposition the granules have a bipolar arrangement. The cells are smaller than the alpha variety and do not show a great change in degree of granulation. The beta cells make up almost exclusively the median border of the islet but are not restricted to this area; a few are found scattered in other regions. At this border they are arranged in definite cords which branch and anastomose. As a rule the elements are at right angles to the long axis of the columns; this often permits two ends of a cell to reach a capillary. This is the cell type that underwent involution after alloxan administration. Normal beta cells are seen in Fig. 4. The cytoplasm of the alpha cells stains a rich orange-yellow color. Their coarse granules stain a reddish-orange; in size they are intermediate between the large zymogen granules of the pancreatic acini and the fine granules of the beta cells. The degree of granulation of these cells normally varies. The nucleus is eccentrically placed and contains little chromatin material. The "D" variety of cell, which is found along the islet periphery, has a cytoplasm which stains blue. The cellular outline is not always well defined, but it can be determined that this cell is larger than both the alpha and the beta cells. Granulation is very fine and a light blue. Cells containing a very small number of granules are numerous. The nucleus is large and densely chromatic. It is centrally placed and also stains blue; one distinct nucleolus is found. Agranular "C" type cells were not present.

A differential cell count was not made but a close examination gives the impression that the alpha cells are more abundant than the beta variety. The "D" cells make up the smallest percentage of islet cells.

## Experimental Results.

In the three series of experiments the reactions of the females and males to alloxan were essentially the same. Most differences that did occur were no greater than those found between individual animals of the same sex who received identical treatment. To avoid repetition, males and females of the same series are grouped together; where differences existed they are listed separately. No difference in the histological detail of the exocrine or endocrine pancreas was noted between gravid and non-gravid females. Except where specifically noted, the alpha, "D" islet cells and the pancreatic acinar cells were uninjured.

*Series I* (0.05%):

Within an hour of placing the fish in the alloxan solution all the females went to and remained at the surface. The males acted similarly after a lapse of five hours. That they were able to swim and reach the bottom was proved by their doing so when the side of the tank was tapped. When quiet prevailed they again rose to the surface. It appeared that they suffered a respiratory distress and sought a greater oxygen supply.

The two males and the female found dead at the 10 hour period were not suitable for a histological study. The islets of three of the four fish sacrificed at this time showed a very definite increase in capillary spaces and beta cell nuclei chromaticity. With eosin the cytoplasm of these cells stained more homogeneously than that of normal cells. Granulation was little changed and could be seen in all cells. The islet of the fourth fish, a female, showed an increase in vascularity and had a few deep-staining nuclei. No change was noted in any other organ.

In the 10-20 hour interval two females and two males were found dead. Microscopic examination showed advanced decomposition, indicating they had been dead for a number of hours. They were not suitable material for study. The islet of each of the four fish sacrificed at this time presented a much more advanced stage of degeneration than at the 10 hour interval. High power examination revealed a very intense hyperchromasia and condensation of the beta cell nuclei; in some areas nuclear fragmentation was also apparent. Degranulation in various degrees was evident; a range from complete degranulation to an almost normal complement was seen. Cellular arrangement was modified and continuity of the columns of cells was interrupted by shrinkage of cells. Liver parenchyma was normal. Hemosiderin in amounts greatly exceeding the normal was found in the liver and in the kidney. The latter organ was in all other respects histologically normal.

By 30 hours six females and six males had died; these were discarded because of decom-

position. At 40 hours a moribund female fish was sacrificed. Most of the beta cells were completely disintegrated, in some sections only an eosinophilic cellular debris remaining. A few remaining cells became rounded and shrunken. These were grouped in small numbers. In these cells the cytoplasm was almost colorless and completely degranulated and their nuclei were very deep-staining. The pancreatic acinar cells showed a lighter staining cytoplasm than normally seen. A few of these cells were vacuolated. The liver at this time presented small localized lesions. In some areas of this organ only shrunken parenchyma cells and a connective tissue stroma were seen. Occasional vacuoles were also found. Hemosiderin in great masses in the liver, veins of the liver, and about the kidney tubules was very prominent; so much was massed in the spleen that the cellular elements of the organ were obscured. The kidney of this specimen presented no signs of injury.

*Series II* (0.025%):

In this series there was little immediate effect on the well-being of the fish. After the second day they ate little and became lethargic.

At the 10 hour period one male appeared essentially normal and the only islet change detectable even with a high magnification systematic examination was an increased vascularity. In addition to a capillary dilation the other three fish showed cellular changes within the islet. In most of the cells the nuclei were so hyperchromatic that a reticulum was obscured. Granulation as seen with the azan stain did not seem to be altered. The ends of the beta cells had become rounded, thus giving the cells a more nearly rectangular shape. The kidney tubules were unimpaired histologically. The liver parenchyma appeared normal but an abnormally large amount of hemosiderin was in the organ.

After an elapse of 20 hours one male was found dead and was discarded because of advanced decomposition. In all killed specimens degenerate changes were now definite and more advanced than at the previous interval. Beta cell nuclei were pycnotic with no structure visible. Cytoplasmic degranulation was in progress; cells totally devoid of granules, as well as cells with a nearly normal amount of granules, were noted. In still other cells a clumping or coalescence of granules had taken place. Cellular shrinkage was so advanced that the individual cells in some sections were detached and separated from one another by large spaces. The mesonephros epithelium showed a slight reduction in height in three specimens, a male being the exception. Localized areas of cell shrinkage were present in the liver of a male and female. The amount of hemosiderin was greatly increased in the livers of all the specimens. This substance was also found around the kidney tubules.

One female fish died in the 30-44 hour interval; this was discarded because of decomposition. In all four animals sacrificed at the 44 hour period, the beta cell nuclei were hyperchromatic and caryorrhexis was evident in some sections. Degranulation was near the terminal stages and many cells totally devoid of granules were seen. With eosin the cytoplasm was clear and stained more homogeneously than at the earlier involution stages or in the normal cells. With azan stain many of the cells were colorless or pale blue. Cell shrinkage was so pronounced that the cells were separated from one another; in some areas they were arranged in irregular compact masses as in Fig. 9. The livers of the four fish showed small loci of cell shrinkage; the nuclei of these elements were normal. As previous, abnormally large amounts of hemosiderin were found in this organ. This substance was also present about the kidney tubules, the epithelium of which was reduced in height.

Beta cell caryorrhexis and cytolysis had taken place in the 44-70 hour interim. Nuclei, cell boundaries and granules were not found at this time. An acidophilic debris had replaced the cells. Alpha cells bordering these areas were swollen but presented no degenerate changes or mitotic figures. Lowering of kidney epithelium height was evident in all four animals. The livers were histologically the same as at 44 hours.

After 5 days neither intact beta cells nor an acidophilic debris were seen. Instead, spaces near the marginal border, the area formerly occupied by the beta cell columns, were observed. Kidney epithelium was now so reduced that it resembled the low cuboidal or the simple squamous type. This change is seen by comparing Fig. 12 with Fig. 13. In the lumen of a few tubules a pale-staining eosinophilic substance appeared. Slight vacuolations were noted in the livers of two fish, the other two presenting the cell shrinkage seen after 44 hours. The hemosiderin deposit was increased in all of the livers. This compound was also massed about the mesonephros tubules of one fish. In this specimen the splenic cells were masked by the great amount of hemosiderin deposited in the organ.

The spaces seen in the islet at the 5 day interval were still apparent on the seventh day. No multiplication or invasion of the area by other cell types had taken place. The histological structure of the kidney was about the same as at the 5 day interval, the only changes discernible being an increased amount of hemosiderin and the presence of an intralumen oxyphilic substance. Vacuolations and small localized lesions were apparent in the liver of one fish; small areas lacking intact cells were found throughout the livers of the other three.

At 9 days the histological picture of all organs was about the same as that seen at the seventh day. Abnormally large, dense black osmophilic droplets at the peripheral areas of the liver suggested that a fatty infiltration of this organ was taking place.

*Series III* (0.013%):

All fish swam about, took food and gave every evidence of being in good health until the third day. After that time little food was taken, the fish became quiescent and sought the corners of the tanks.

Of the four fish examined at the 10 hour interval, one female presented an essentially normal histological picture. As seen under low magnification the main islet change in the other three specimens was an increased blood supply. Capillary dilation was visible and erythrocytes were more abundant than normally found in the structure. A few hyperchromatic nuclei were observed with higher magnification. Beta cell granulation remained within the normal range. Both the kidney and the liver were unchanged in all specimens.

By 20 hours practically all of the beta cell nuclei of all the specimens were pycnotic. Capillary dilation was evident. High power examination revealed that the granulation of many cells was slight, but it could not be determined if it was still within the normal range or was an abnormality. The liver parenchyma of all fish was normal, a hemosiderin deposition greater than normal being noted in the gland. The kidneys presented no abnormalities.

At the 44 hour interval the beta cell nuclei were hyperchromatic. Caryolysis was not seen. With the azan stain a great diminution of granules was noted in many cells of three fish; the other fish, a male, presented a doubtful picture in this regard. The cytoplasm of the beta cells undergoing degranulation stained very pale with eosin. Cell shape alteration was in progress and many rounded cells were seen. The columnar arrangement of cells near the gall bladder was impaired and in some sections the elements were now in clusters. The kidney epithelium height was not reduced, but the cytoplasm stained lighter than normal. The livers of two fish (one male and one female) were normal except for a greater than normal deposition of hemosiderin. The parenchyma of the other livers had a looser arrangement than that regularly seen.

After 70 hours the beta cell nuclei were shrunken and deep-staining. Granulation was sparse and only a few granules could be seen in a small number of cells. In the degranulated cells the cytoplasm stained homogeneously and blue with the azan stain. Islet architecture was not within the normal range. Definite columns of cells were replaced by clusters of crumpled cells with pycnotic nuclei. The exocrine cells in all, except one fish (a male), were normal. In the latter the cytoplasm was degranulated and pale-staining. The kidneys of all fish presented the same details as at 44 hours. Three of the livers had some shrunken cells and a slight vacuolation; the other (from a female) was normal. All four showed an increased hemosiderin deposit in this organ and around the kidney tubules.

On the fifth day the marginal border of the islet which normally contains the beta cells, was without intact cells. An eosinophilic cellular debris and cytoplasmic masses without nuclei or cell boundaries were the only remains of cells to be found. The kidney epithelium was slightly reduced and vacuolated; the cytoplasm stained pale. An eosinophilic colloid-like substance was present in the lumen of the tubules. Although the liver parenchyma of all of the fish was shrunken, the nuclei of the hepatic cells were normal. Hemosiderin deposition in both the liver and the kidney was again greater than normal.

By the seventh day the beta cell debris was replaced by a fine connective tissue stroma. The alpha cells adjacent to the area were slightly swollen, but their granulation was not affected. Mitotic figures were not seen in the islet. The kidney epithelium of all specimens was reduced in height and the nuclei of these elements now were hyperchromotic. A granular and reticular material was noted in the lumen of the tubules. Cytoplasmic shrinkage and vacuolation was seen in varying degrees in all of the livers; in fact, areas consisting only of connective tissue were found. A great hemosiderosis was also present in the organ. These changes can be seen by comparing Fig. 10 and Fig. 11.

The main feature demonstrated on the ninth day was solid, dense black osmophilic droplets at the peripheral areas of the liver. These were present in all of the specimens.

The male and female fish that were maintained until death, died on the forty-first and thirty-ninth days respectively. During this time they were sluggish and took little food. At the time of death a loss of weight was apparent, their bodies had greatly thinned and attained a degree of transparency. Both fish were found dead and were not suitable for study because of decomposition.

## Discussion.

That the teleostean fishes possess the homologue of the mammalian islands of Langerhans was postulated by Diamare in 1899. The studies of Massari (1898), Rennie (1903, 1905) and especially that of McCormick (1926) demonstrated that such structures are found in many different species of both fresh water and marine teleosts. As a rule the islets are fewer in number and are larger than those found in mammals. The number of islets varies with the species. For example, one is found in *Gadus callarias* Linnaeus, while about 50 are found in *Ameiurus lacustris* (Walbaum) (McCormick, 1926). When more than one islet exists it is usually noted that one of the number is bigger than any of the others and that it may in some cases be seen with the naked eye. Rennie (1903) termed the largest islet the "principal islet." In the present study it was found that the guppy has only one islet and that it can in large specimens be seen macroscopically.

TABLE I.

Histological Changes After Alloxan Administration.

| | Series I. 0.05% | Series II. 0.025% | Series III. 0.013% |
|---|---|---|---|
| 10 hours | Islet capillaries dilated.<br>B nuclei hyperchromatic. | Islet capillaries dilated.<br>B nuclei deep staining.<br>Hemosiderin in liver. | Islet capillaries dilated. |
| 20 hours | B nuclei condensed, some caryorrhexis.<br>B cell degranulation and shrinkage in progress.<br>Hemosiderin in liver and kidney. | B nuclei pycnotic.<br>B cell degranulation and shrinkage in progress.<br>Slight reduction of kidney epithelium height.<br>Hemosiderin in liver and kidney. | B nuclei pycnotic.<br>Hemosiderin in liver. |
| 40 hours | B cell disintegration.<br>Liver lesions.<br>Hemosiderin in liver, kidney and spleen. | | |
| 44 hours | | Some B nuclei fragmentation.<br>Advanced B cell degranulation.<br>Pronounced B cell shrinkage.<br>Cell shrinkage in liver.<br>Kidney epithelium height reduced.<br>Hemosiderin in liver and kidney. | B nuclei pycnotic.<br>B cell degranulation and shrinkage in progress.<br>Hemosiderin in liver. |
| 70 hours | | B cell caryorrhexis and cytolysis.<br>Kidney epithelium height reduced.<br>Hepatic cell shrinkage.<br>Hemosiderin in liver and kidney. | B nuclei pycnotic.<br>B cell granulation sparse.<br>B cell break-up.<br>Liver vacuolated.<br>Hemosiderin in liver and kidney. |
| 5 days | | No intact B cells.<br>Marked reduction of kidney epithelium height, intralumen substance present.<br>Cell shrinkage and vacuolation in liver.<br>Hemosiderin in liver, kidney and spleen. | No intact B cells.<br>Kidney epithelium height reduced with intralumen substance present.<br>Hemosiderin in liver and kidney. |
| 7 days | | Marginal area of islet devoid of cells.<br>Kidney epithelium height reduced.<br>Lesions and vacuolations in liver<br>Hemosiderin as at 5 days. | As at 5 days plus liver lesions. |
| 9 days | | Large osmophilic droplets in liver. | Large osmophilic droplets in liver. |

Some early workers tried to relate the fish islet to the endocrine system and carbohydrate metabolism. Diamare in 1905 attempted the preparation of a glucose-repressing extract from the islet tissue of different species of fish. Years later MacLoed[2] (1922) and McCormick & Noble[3] (1925) succeeded in obtaining insulin from a variety of teleostei. Jackson (1922) demonstrated by the differential solubility method of Lane the presence in fish of two cell types having the same characteristics as the alpha and beta cells of the mammalian islands. Thus on both histological and physiological grounds it was shown rather conclusively that the islet of the teleost is represented in mammals by the islands of Langerhans. Bowie in 1924 continued and extended the cytological work by using a differential staining method; at that time he demonstrated three types of granular cells in the islet of *Neomaenis griseus*. He termed them alpha, beta and gamma cells. In the present report the existence of three types of granular cells is also recorded but the data are not in strict accord with that of Bowie's, the main difference being in the granular detail. Bowie claimed that the beta cell granules are larger than the alpha cell granules and that they may even approach the size of the zymogen granules of the exocrine pancreatic cells. The reverse situation was found to prevail in *Lebistes reticulatus*. Bowie's description of the gamma cell corresponds rather well with that given here for the "D" cell. If we allow for the fact that different techniques and a very different fish were used, it is possible that the same cell types are to be found in both *Neomaenis griseus* and *Lebistes reticulatus*.

Bensley (1911) noted that in addition to the alpha and the beta cells an agranular "C" cell is present in the guinea pig pancreas. For many years a controversy as to whether this "C" cell is a fundamental cell type or is peculiar to the guinea pig has been waged. In most of the more recent investigations the agranular cell has not been reported to exist in animals other than the guinea pig. In Bowie's report no mention was made of the "C" cell type. The present study, employing a differential staining method that is capable of demonstrating such a cell, failed to reveal any type of granular cell. The "D" cell type has been described in man (Bloom, 1931), in many other mammals and in the elasmobranchii (Thomas, 1937, 1940). It seems that the three granular cells, the alpha, the beta and the "D" cells, are the more fundamental islet components.

It is evident from the experimental results of this report that islet cell injury similar to that which has been reported to take place in mammals can be produced in the teleost *Lebistes reticulatus* by the immersion of the fish in an alloxan solution of suitable concentration. It is to be noted that the rate at which the beta cell cytological changes were produced and the time of death of the fish depended upon the alloxan dosage employed. There also exists an initial variation in the affectibility of individual fish to the same concentration of the drug. The deviations may be a reflection of a difference in the activity of the individual cells at the time they are first acted upon by the alloxan. In the series of experiments of this study several early deaths occurred when a concentration of 0.05% alloxan solution was used. It appears that this concentration is very close to, if not the actual upper sub-lethal dose for the guppy by the immersion method. The early deaths were not convulsive and from the actions of the fish in seeking the surface they may in part be attributed to an interference with respiration. It has been shown by Shipley & Rannefield (1945) and Houssay *et al* (1946) that repeated, small, sub-diabetogenic doses may produce islet necrosis similar to that caused by a large massive dose. The immersion method as used in this experiment could theoretically produce an additive effect. Therefore it is not possible to come to any conclusion as to whether or not the 0.013% alloxan series represents the lowest possible beta cell toxic concentration for *Lebistes reticulatus*.

It is of interest to note that the islet changes in the guppy, even with the highest drug concentration used, do not become apparent as soon as they do in the mammalian forms studied. In most mammals the injuries are rapidly produced. In many studies nuclear changes, cytoplasmic degranulation and cellular fragmentation have been reported to take place within a few hours (Duff & Starr, 1944; Dunn *et al*, 1944); in fact, Hughes *et al* (1944) claimed that the initial islet injury in the rat occurs within five minutes of the alloxan administration. In the present study similar changes, though not to such an advanced stage, were noted after a lapse of 20 hours at the highest concentration. Whether the lag is innate or is a reflection of slow assimilation because of the immersion method might possibly be determined by administering alloxan by injections. Seiden (1945) also noted a lag when the frog was used as an experimental animal; he administered alloxan by injections. It may well be that the longer interval between the drug administration and the produced necrotic effects are in some way a reflection of a lower metabolic rate of the cold blooded vertebrates.

Although all three concentrations eventually produced the same results, the lower concentration required a longer time to do so. This slower action provided more information and permitted a more detailed analysis of the involution stages; therefore the main interest centers about the fishes that survived at the lower concentrations. The earli-

[2] *Anguilla rostrata* (LeSueur), *Myoxocephalus octodecimspinosus* (Mitchill), *Myoxocephalus scorpius* (Linnaeus), *Lophius piscatorius* Linnaeus.

[3] *Pollachius virens* (Linnaeus), *Gadus callarias* Linnaeus, *Melanogrammus aeglefinus* (Linnaeus), *Merluccius bilinearis* (Mitchill), *Hippoglossus hippoglossus* (Linnaeus), *Pseudopleuronectes americanus* (Walbaum), *Hemitripterus americanus* (Gmelin), *Cyclopterus lumpus* Linnaeus, *Macro americanus* (Bloch & Schneider).

est changes noted were an increased vascularity, a dilation of the islet capillaries and a hyperchromasia of the nuclei of the beta cells. These alterations were followed by a change in the degree of granulation and in the staining quality of the cytoplasm. Soon after degranulation had started cell shrinkage took place; the latter modification caused a disturbance of the columnar arrangement of the cells. Finally, complete caryolysis and cytolysis occurred. The time of death of the individual cell can not be determined with a great degree of certainty from this study, but it most probably took place at the time of cell shrinkage. The lack of both mitotic figures and cell proliferation in the islet indicates that the beta cell damage is irreversible.

It is well known, as indicated above, that insulin having physiological characteristics of mammalian insulin can be obtained from teleost islets. Having shown that the cell type which is generally conceded to be the producer of insulin is present in the guppy, and that these cells were destroyed, and knowing that a removal of the islet cells of the teleost results in a diabetic state (Simpson, 1926), we may assume that the fish in this experiment became diabetic.

A review of the literature shows that the consensus of opinion is that island injury by alloxan is restricted to the beta cells. Several investigators claim that some alpha cells may also degenerate. Saviano (1947b), using two different species of fishes, reported that the principal injury was suffered by the dark-staining cells (Mallory-Heidenhaim-Gomori stain). He termed this cell type the alpha cell. In the present experiment the elements staining dark are considered to be the beta cells and the lighter elements are termed alpha cells. This terminology is based on criteria of cytological details listed above and generally accepted; it is substantiated by the differential reaction of the cell types to alloxan. Although a slight swelling of the alpha cells adjacent to the area of the injured beta cells was observed in several preparations, no definite signs of degeneration of these cells were discernible. The marked difference in the reaction of the alpha and the beta cells to alloxan is significant, and may be considered an indication of a a fundamental difference in the composition and in the physiological role of the two cell types.

A histological deviation from the usual cellular detail of the exocrine pancreatic cells was noted in two of the fish examined. In both a degree of degranulation, with a resulting lighter and more homogeneous staining of the cytoplasm, had taken place. The nuclei of these cells were unchanged. The sections suggested a state of exhaustion similar to that produced by a period of high secretory activity, rather than cells undergoing a degenerative process.

It has been found that in some higher forms a large dose of alloxan may lead to severe acute lesions of the kidney. Vacuolation and desquammation of the tubules is common. Goldner & Gomori (1943) and Houssay (1946) likened the injury to that caused by mercury. There exists a relationship between the drug dose and the renal damage; often the nephrotoxic dose is greater than the minimum diabetogenic dose (Goldner & Gomori, 1943). By taking advantage of this relationship a diabetic state without renal damage may be produced in some forms. Fish in all three series of this experiment underwent kidney tubule modifications. A reduction in epithelial height with an increase in the lumen size (while the outside diameter of the tubule remained constant) was noted. An eosinophilic substance within the lumen was present in some specimens. These alterations are very similar to those described in studies of mammals. It is thought that the mammalian tubule damage is due to a direct sensitivity of the structures to the drug rather than being a consequence of islet cell alteration; for had the changes been caused by the produced permanent islet necrosis, it is not likely that the kidney would have reverted both functionally (Bennett & Behrens, 1946) and histologically (Ruben & Yardumian, 1946) to the normal state. In the present study the kidney remained histologically abnormal throughout the observed period, but it must be remembered that here, by the immersion method, the fish were constantly exposed to the drug and that even if the tubules are capable of repair they may be prevented from doing so by the uninterrupted exposure to the toxic substance.

Localized hepatic lesions in the form of cytoplasmic shrinkage, cellular disintegration and collapsed sinusoids were apparent in some preparations. An inflammatory reaction was not present. The livers of the specimens which were fixed with Flemming's fluid contained abnormally large black droplets suggestive of a fat infiltration. Because the normal liver contains much oil it is difficult to determine with osmic acid whether this represented an extreme fatty infiltration of the organ. The Bouin-fixed, hematoxylin-eosin stained liver tissue of fish killed at the later intervals presented large round vacuoles not seen in the normal liver; this is also suggestive of a fatty infiltration. The first mentioned lesions seem to be a direct alloxanic effect rather than a result of a possible diabetic state, for they developed in the time that the islet cells were still undergoing change. The fat infiltration was noted several days after the start of the experiment, therefore it can not be determined if the change was due primarily to alloxan or to a disturbed metabolism.

Another complication following the administration of alloxan is an increased hemosiderosis in some animals. Lowered erythrocyte counts, hemoglobinemia and hemoglobinuria were recorded to take place in rabbits (Kennedy & Lukens, 1944) and in rats (Gyorgy & Rose, 1948). Herbut *et al* (1946) noted a

hemochromatosis in rabbits after alloxan treatment. In the present study greater than normal iron deposits, indicative of hemosiderin, were deposited in the liver, kidney, large blood vessels and the spleen. Since no blood counts were made we must consider two hypotheses to explain the abnormally large amount of hemosiderin. First, the hemosiderin deposition is the resultant of a decrease in excretion of the compound due to an impairment of the excretory mechanism. Second, the accumulation results from an excessive production of erythrocyte breakdown products. The fact that the hemosiderin deposits were observed before the kidney and liver damage became apparent suggests that the latter hypothesis may explain the findings but does not completely eliminate the first one. It may well be that the deposition was at first due to an excessive hemolysis and that the condition was later aggravated by disturbed renal and hepatic function. The works of Kennedy & Lukens (1944) and of Gyorgy & Rose (1948) are excellent evidence for an increased hemolysis in the forms they studied. Kennedy & Lukens also reported that the effects are reversible. Gyorgy & Rose proved that in rats the hemoglobinuria which usually follows a diabetogenic dose of alloxan may be prevented by maintaining the animals on a diet rich in tocopherol. The increased hemolysis in the rat is therefore independent of the other effects of alloxan. Whether or not the same condition exists in the species of fish reported in this study can be determined only by further study.

The above reactions indicate that alloxan, or a produced derivative, is a multi-factor agent.

## Summary.

1. The teleost *Lebistes reticulatus* has pancreatic endocrine epithelial cells condensed into one compact nodule.

2. The islet consists of three types of granular cells: the alpha, the beta and the "D" cells. The alpha cells are more abundant than the beta variety. The "D" cells are the least numerous. An agranular cell type is not present.

3. The beta cells of the islet undergo nuclear pycnosis, cytoplasmic degranulation and complete disintegration after the administration of alloxan. The alpha and the "D" cells are not subject to necrosis and remain undamaged.

4. After exposure to alloxan the kidney epithelium height is reduced; in consequence of this alteration the size of the lumen of the tubules is increased while the outside diameter of the structures remains normal.

5. Liver parenchymatous injury occurs after alloxan treatment. Necrosis and a degree of fat infiltration of the organ take place.

6. A large amount of hemosiderin is found intravsacularly and in the liver, kidney and spleen of the alloxan-treated fish.

7. No sex difference is noted for any of the above reactions.

## Literature Cited.

Banerjee, S.
1944. Alloxan Diabetes in Monkeys. *Lancet*, 2: 658-659.

Bennett, L. L. & T. Behrens
1946. Alloxan-Induced Azotemia in Rats. *Proc. Soc. Exper. Biol. and Med.*, 62: 5-6.

Bensley, R. R.
1911. Studies on the Pancreas of the Guinea Pig. *Amer. Jour. Anat.*, 12: 297-388.

Biasotti, A. & J. Porto
1945. Influencia del Aloxano en el *Bufo arenarum* Hensel. *Rev. Soc. Argent. de Biol.*, 21: 63-73.

Bloom, W.
1931. A New Type of Granular Cell in the Islets of Langerhans of Man. *Anat. Rec.*, 49: 363-370.

Bowie, D. J.
1924. Cytological Studies of the Islets of Langerhans in a Teleost, *Neomaenis griseus*. *Anat. Rec.*, 29: 57-73.

Corkill, A. B., P. Fantl & J. F. Nelson
1944. Experimental Diabetes by Injection of Alloxan. *Med. Jour. Australia*, 31: 285-286.

Diamare, V.
1895. I Corpuscoli Surrenali di Stannius ed i Corpi del Cavo Abdominale dei Teleostei. *Boll. Soc. Nat. Napoli*, 9: 10-24.
1899. Studii Comparativi Sulle Isole di Langerhans del Pancreas. *Intern. Monatsschr. Anat. Phys.*, 16: 155-209.
1905. Studii Comparativi Sulle Isole di Langerhans del Pancreas. *Ibid.*, 22: 127-187.

Di Pietro, A. & A. F. Cardeza
1946. Necrosis Pancreatica y Esteatonecrosis por Aloxano. *Rev. Soc. Argent. de Biol.*, 22: 288-298.

Duff, G. L., G. McMillan & D. C. Wilson
1947. Hydropic Changes in Pancreatic Ductules and Islets in Alloxan Diabetes in the Rabbit. *Proc. Soc. Exper. Biol. and Med.*, 64: 251-255.

Duff, G. L. & H. Starr
1944. Experimental Alloxan Diabetes in Hooded Rats. *Proc. Soc. Exper. Biol. and Med.*, 57: 280-282.

Dunn, J. S., E. Duffy, M. K. Gilmour, J. Kirkpatrick & N. G. B. McLetchie
1944. Further Observations on the Effects of Alloxan on the Pancreatic Islets. *Jour. Physiol.* 103: 233-243.

Dunn, J. S. & N. G. B. McLetchie
1943. Experimental Alloxan Diabetes in the Rat. *Lancet*, 2: 384-387.

Dunn, J. S., H. L. Sheehan & N. G. B. McLetchie
1943. Necrosis of Islets of Langerhans Produced Experimentally. *Lancet*, 1: 484-486.

GOLDNER, M. G. & G. GOMORI

1943. Alloxan Diabetes in the Dog. *Endocrinology*, 33: 297-308.

1944a. Studies on the Mechanism of Alloxan Diabetes. *Ibid.*, 35: 241-248.

1944b. Mechanism of the Diabetogenic Action of Alloxan. *Proc. Soc. Exper. Biol. and Med.*, 55: 73-75.

1945. Effect of Alloxan on Carbohydrate and Uric Acid Metabolism of the Pigeon. *Ibid.*, 58: 31-32.

GOMORI, G.

1939. Studies on the Cells of the Pancreatic Islets. *Anat. Rec.*, 74: 439-460.

GYORGY, P. & C. S. ROSE

1948. Effect of Dietary Factors on Early Mortality and Hemoglobinuria in Rats Following Administration of Alloxan. *Science*, 108: 716-718.

HARRIS, V. D. & W. J. GOW

1894. Note Upon One or Two Points in the Comparative Histology of the Pancreas. *Jour. Physiol.*, 15: 349-360.

HERBUT, D. A., J. S. WATSON & E. PERKINS

1946. Hepatic and Renal Necrosis of Alloxan Diabetes of Rabbits. *Arch. Path.*, 41: 516-525.

HOUSSAY, B. A., R. F. BRIGNONE & P. MAZZOCCO

1946. Diabetes Metaaloxanica en el Perro. *Rev. Soc. Argent. de Biol.*, 22: 195-231.

HOUSSAY, B. A., O. ORIAS & J. G. SARA

1945. Acción del Aloxano sobre la Glucemia del Perro. *Rev. Soc. Argent. de Biol.*, 21: 30-44.

HUGHES, H., L. L. WARE & F. G. YOUNG

1944. Diabetogenic Action of Alloxan. *Lancet*, 1: 148-150.

JACKSON, S.

1922. The Islands of Langerhans in Elasmobranch and Teleostean Fishes. *Jour. Metab. Res.*, 2: 141-147.

JACOBS, H. R.

1937. Hypoglycemic Action of Alloxan. *Proc. Soc. Exper. Biol. and Med.*, 407-409.

JARRETT, I. G.

1946. Alloxan Diabetes in the Sheep. *Australian Jour. Exper. Biol. and Med.*, 24: 95-102.

KENDALL, F. E., W. MEYER, L. LEWIS & J. VICTOR

1945. Alloxan Diabetes in Rabbits. Production of Hypercholesterolemia, Hyperlipemia and Adrenal Cortical Lesions. *Proc. Soc. Exper. Biol. and Med.*, 60: 190-195.

KENNEDY, W. B. & F. D. LUKENS

1944. Observations on Alloxan Diabetes. *Proc. Soc. Exper. Biol. and Med.*, 57: 143-149.

LAGUESSE, E.

1895. Sur le Pancréas du Crenilabre. *Rev. Biol. du Nord de la France*, 7: 343-363.

LAZAROW, A.

1946. Protective Effect of Glutathione and Cysteine Against Alloxan Diabetes in the Rat. *Proc. Soc. Exper. Biol. and Med.*, 61: 441-447.

LAZAROW, A. & S. PALAY

1946. The Production and Course of Alloxan Diabetes in the Rat. *Jour. Lab. and Clin. Med.*, 31: 1004-1015.

MASSARI, G.

1898. Sul Pancreas dei Pesci. *Rend. R. Accad. dei Lincei*, 7 (5): 134-137.

MACLOED, J. J.

1922. The Source of Insulin. *Jour. Metab. Res.*, 2: 149-172.

MCCORMICK, N. A.

1926. The Distribution and Structure of the Islands of Langerhans in Certain Fresh Water and Marine Fishes. *Trans. Roy. Canad. Inst.*, 15: 57-81.

MCCORMICK, N. A. & E. C. NOBLE

1925. The Yield of Insulin from Fish. *Contrib. Canad. Biol.*, new ser., 2: 117-127.

MIRSKY, A.

1945. Alloxan Administration to the Duck. *Proc. Soc. Exper. Biol. and Med.*, 59: 35-37.

RAMOS, J. G.

1944. Contribucion al Conocimiento de la Farmacologia de la Aloxana. *Rev. Soc. Mexicana de Hist. Nat.*, 5: 25-34.

RENNIE, J.

1903. On the Occurrence of a "Principal Islet" in the Pancreas of Teleostei. *Jour. Anat. Phys.*, 37: 375-378.

1905. The Epithelial Islets of the Pancreas in Teleostei. *Quart. Jour. Micr. Sci.*, 48: 379-406.

RUBEN, J. A. & K. YARDUMIAN

1946. Diabetes Produced by Feeding Alloxan to Cats. *Science*, 103: 220-221.

SAVIANO, M.

1947a. Ricerche Sull'azione Diabetogena Dell'allossana Nei Selaci. II. Ulteriori Osservazioni sul Comportamento Della Glicemia ed Esame Istologico del Pancreas. *Boll. Soc. Nat. Napoli*, 23 (12): 1290-1295.

1947b. Ricerche Sull'azione Diabetogena Dell'allossana Nei Teleostei. II. Osservazioni Istologiche sul Tessuto Insulare. *Ibid.*, 23 (12): 1300-1304.

SEIDEN, G.

1945. The Response of the Pancreatic Islands of the Frog (Rana pipiens) to Alloxan. *Anat. Rec.*, 91: 187-198.

SHIPLEY, E. G. & K. H. BEYER

1947. The Effect of Vagotomy and of Thoracic Sympathectomy on the Blood Glucose Changes in Dogs Given Alloxan. *Endocrinology*, 40: 154-164.

SHIPLEY, E. G. & A. N. RANNEFELD
1945. Glucose Tolerance in Rats Following Repeated Small Doses of Alloxan. *Endocrinology,* 37: 313-321.

SIMPSON, W. W.
1926. The Effects of Asphyxia and Isletectomy on the Blood Sugar of Myoxocephalus and Ameiurus. *Amer. Jour. Physiol.,* 77: 409-418.

STANNIUS, F. H.
1846. Lehrbuch der Vergleichenden Anatomie. Cited from Diamare, 1895, and McCormick, 1926.

THOMAS, T. B.
1937. Cellular Components of the Mammalian Islets of Langerhans. *Amer. Jour. Anat.,* 62: 31-57.
1940. Islet Tissue in the Pancreas of the Elasmobranchii. *Anat. Rec.,* 76: 1-18.

## EXPLANATION OF THE PLATES.

All photomicrographs were taken of tissue fixed in Bouin's fluid; tissue represented by Figs. 4 and 5 were stained with azan, the other figures represent tissue stained with Harris' hematoxylin and eosin.

### PLATE I.

Fig. 1. Parasagittal section of a normal fish showing the islet on the ventral surface of the stomach, anterior to the spleen. × 16.

Fig. 2. Frontal section of a normal fish. The islet is seen on the median line, close to the liver and anterior to the spleen. × 16.

### PLATE II.

Fig. 3. Cross section of a normal fish. The islet is seen on the ventral surface of the stomach adjacent to the liver. × 25.

Fig. 4. Portion of the median border of the islet of a normal fish, consisting almost exclusively of beta cells. These cells are dark and so heavily granulated that the nucleus of some of the cells is not visible. × 1200.

Fig. 5. Portion of the median border of the islet of an alloxan-treated fish. The beta cells are considerably degranulated. × 1200.

### PLATE III.

Fig. 6. Cross section of the islet of a normal fish. Exocrine pancreatic cells are about the islet. At the right of the islet, blood vessels and gall bladder epithelium are visible. × 340.

Fig. 7. Cross section of the islet of an alloxan-treated fish. At the right (the median border of the islet) shrinkage of the beta cells with an opening of spaces between cell cords is marked. A partial encirclement of the islet by pancreatic acinar cells is seen. × 340.

Figs. 8 & 9. Cross section of the islet of an alloxan-treated fish. At the right (the median border of the islet) beta cell degeneration is seen. The cell outlines are indistinct. The normal columnar arrangement of the cells is no longer visible. The cytoplasm is pale-staining and confluent. The greater part of the islet is unaffected; this area consists almost exclusively of alpha cells. Fig. 8, × 310; Fig. 9, × 525.

### PLATE IV.

Fig. 10. Cross section of the liver of a normal fish. × 550.

Fig. 11. Cross section of the liver of an alloxan-treated fish, showing shrunken parenchyma cells and vacuolization. The blood vessel at the upper right contains hemosiderin. × 550.

Fig. 12. Cross section of the kidney of a normal fish. × 170.

Fig. 13. Cross section of the kidney of an alloxan-treated fish. The tubular epithelium is greatly reduced. In the lower right corner two masses of hemosiderin are seen. × 170.

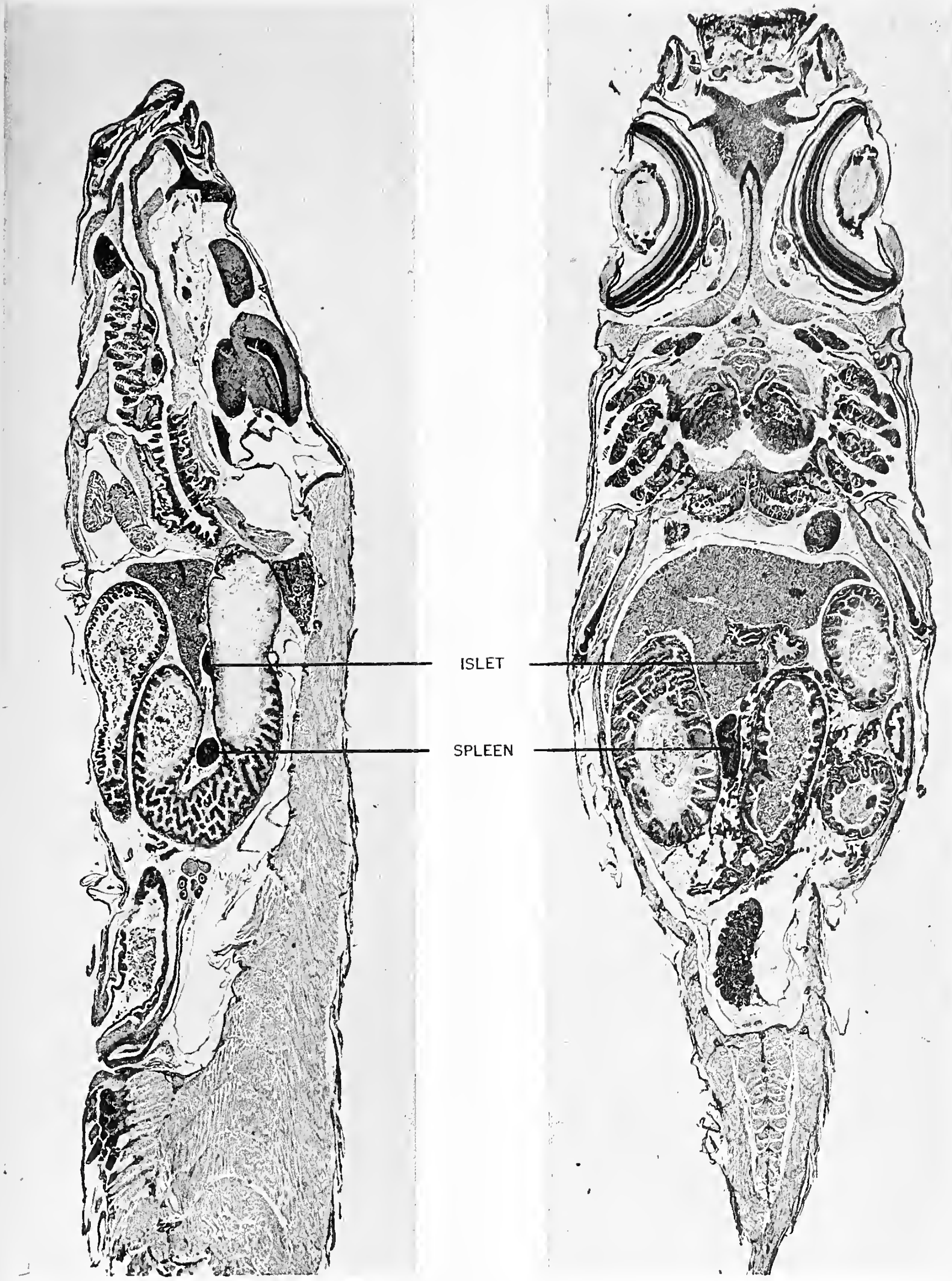



FIG. 1. FIG. 2.

THE EFFECT OF ALLOXAN ON THE PANCREAS, LIVER AND KIDNEY OF THE TELEOST, LEBISTES RETICULATUS, WITH NOTES ON THE NORMAL PANCREAS.

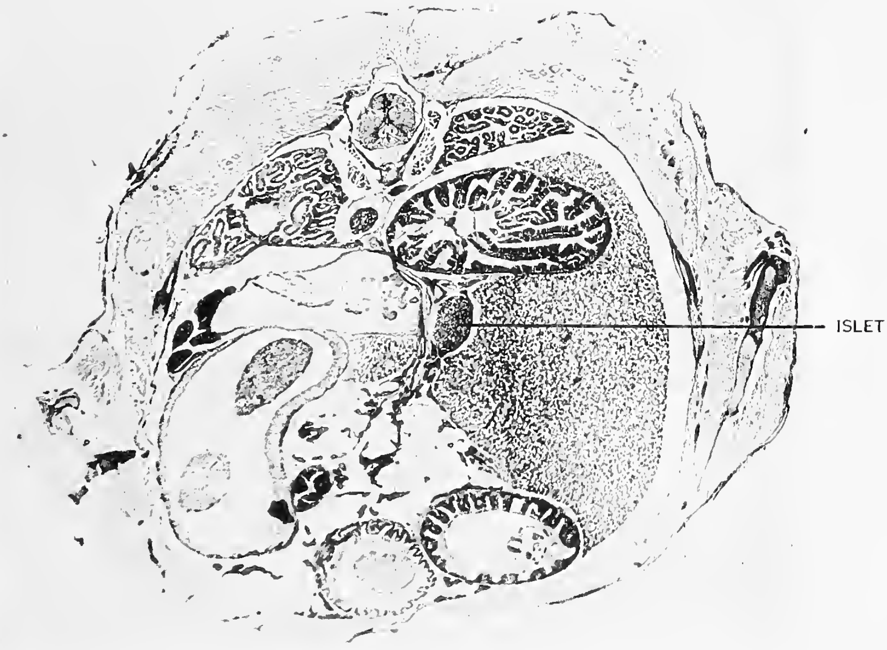



FIG. 3.

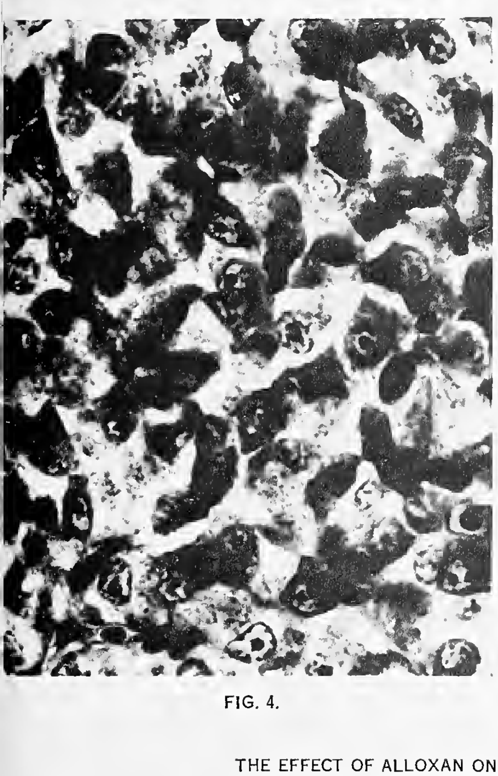


FIG. 4.

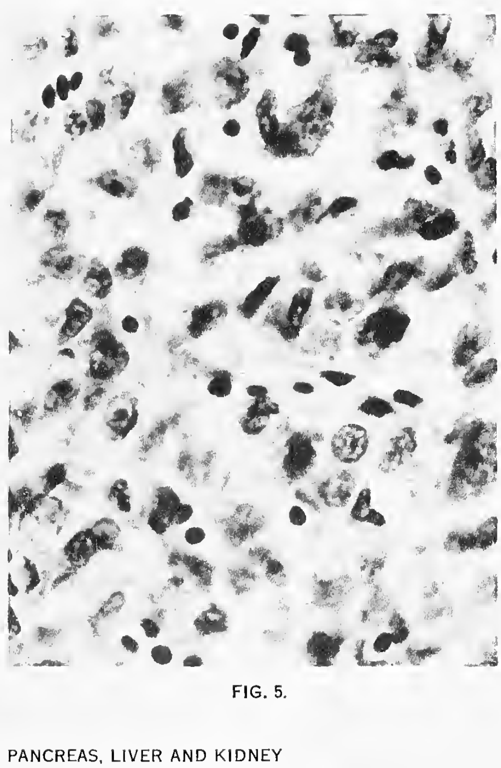


FIG. 5.

THE EFFECT OF ALLOXAN ON THE PANCREAS, LIVER AND KIDNEY OF THE TELEOST, LEBISTES RETICULATUS, WITH NOTES ON THE NORMAL PANCREAS.

FIG. 6.

FIG. 7.

FIG. 8.

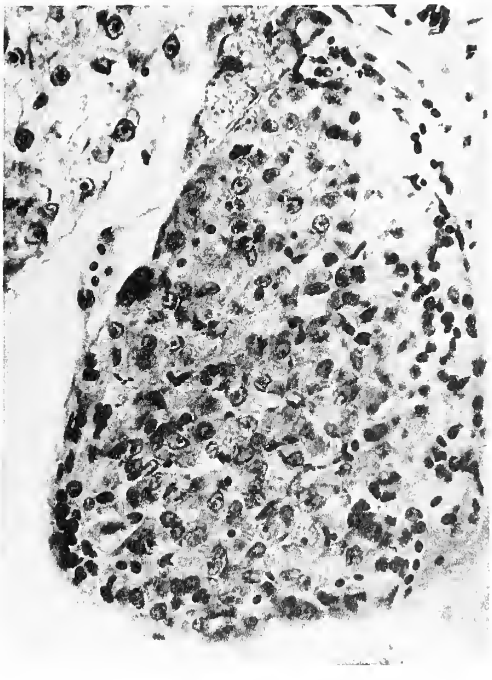


FIG. 9.

THE EFFECT OF ALLOXAN ON THE PANCREAS, LIVER AND KIDNEY OF THE TELEOST, LEBISTES RETICULATUS, WITH NOTES ON THE NORMAL PANCREAS.

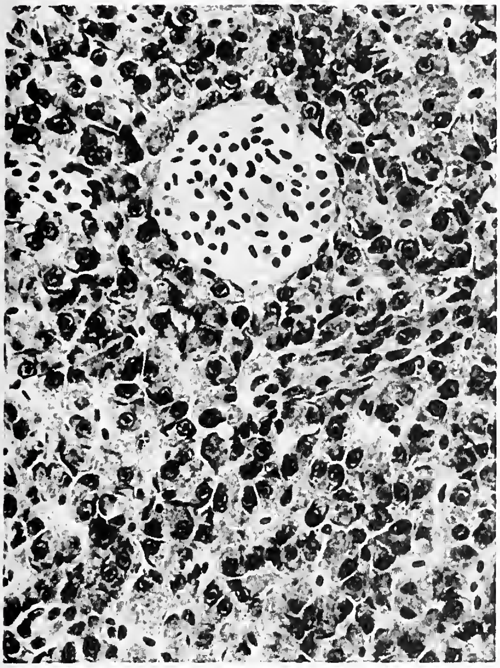


FIG. 10.

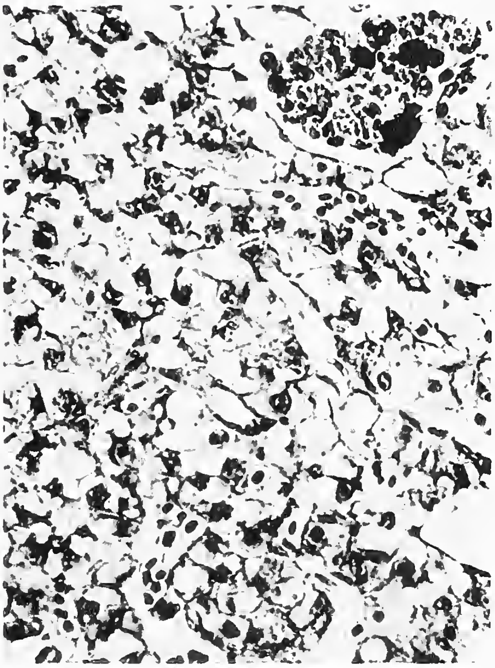


FIG. 11.

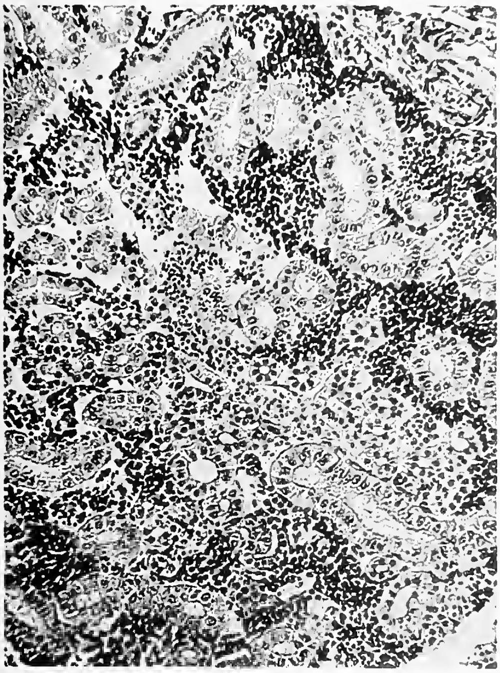


FIG. 12.

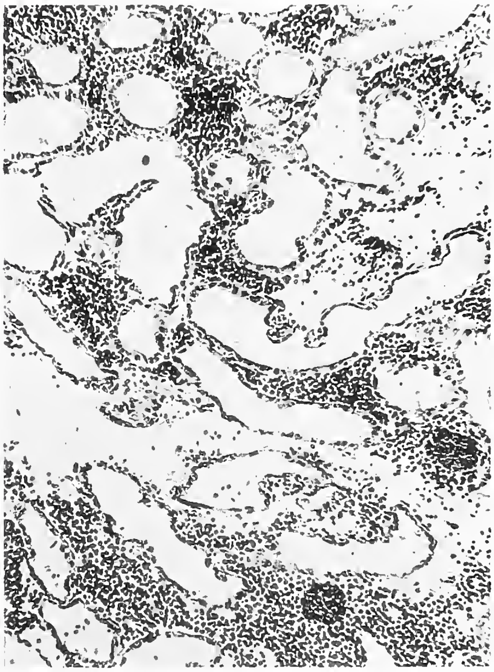


FIG. 13.

THE EFFECT OF ALLOXAN ON THE PANCREAS, LIVER AND KIDNEY OF THE TELEOST, LEBISTES RETICULATUS, WITH NOTES ON THE NORMAL PANCREAS.

# 15.

# An Ecological Study of Helminths of Some Wyoming Voles (*Microtus* spp.) with a Description of a New Species of *Nematospiroides* (Heligmosomidae: Nematoda).[1]

MERLE L. KUNS & ROBERT RAUSCH.[2]

(Text-figures 1-7).

## PROBLEM.

Studies on parasitic infections may be made with special reference to either a parasite or a host group. Taxonomic studies are usually concerned with a group of closely related parasites which may have been collected from a wide variety of hosts. This is the most common method of obtaining data, and is one essential step for the proper understanding of parasite taxonomy. However, another method which involves consideration of the problems of parasitism within a group of closely related hosts, facilitates the understanding of such ecological problems as distribution and control and emphasizes evolutionary and zoogeographic implications. It is this latter approach to the problem of host-parasite relationships in which we have been primarily interested.

It is the purpose of this paper to present data resulting from an ecological study of the helminth parasites of voles of the genus *Microtus* collected during the summer of 1948 from various habitats in the Jackson Hole region of Wyoming.

The ecological aspects of parasitism in mouse-like rodents have until recently received little attention. Elton *et al* (1931) studied the helminths of *Apodemus sylvaticus* L. and reported a correlation of parasitism and age. Rodent parasites were studied in North Carolina by Harkema (1936), with some reference to seasonal fluctuation. An intensive study on the ecology of certain mouse-like rodents in the Transcaucasus region of Russia was carried on by Kirschenblatt (1938). Kirschenblatt's work has been discussed in a previous paper (Rausch & Tiner, 1949). Rankin (1945) studied the helminth parasites of various rodents in the state of Washington. At the present time, the most complete study of the ecology of helminths parasitic in voles is that of Rausch & Tiner (1949), in which several species of parasites are considered.

## OBSERVATIONS AND RESULTS.

Eleven species of parasitic helminths were recovered from 103 representatives of four species of *Microtus* (Cricetidae) collected in the Jackson Hole region of Wyoming. The species of voles considered were *M. pennsylvanicus modestus* (Baird), *M. montanus nanus* (Merriam), *M. longicaudus mordax* (Merriam) and *M. richardsoni macropus* (Merriam). The techniques used in connection with the collection of the parasites was the same as that outlined in previous publications (Rausch & Tiner, 1948; 1949).

Mammal population data were obtained according to the method of Bole (1939). This method consists of saturating representative quadrats of one-half acre (22,500 square feet) with snap traps for a three-day period. This allows for a relative idea of rodent population density per unit area.

The following helminths were collected: *Quinqueserialis hassalli* (McIntosh & McIntosh, 1934); *Andrya primordialis* (Douthitt, 1915); *A. macrocephala* (Douthitt, 1915); *Paranoplocephala infrequens* (Douthitt, 1915); *P. variabilis* (Douthitt, 1915); *P. borealis* (Douthitt, 1915); *Hymenolepis horrida* (von Linstow, 1900); *Heligmosomum costellatum* (Dujardin, 1845); *Nematospiroides microti* n. sp.; *Syphacia obvelata* (Rudolphi, 1802); and *Trichuris opaca* Barker & Noyes, 1915. Of these, all are known to be common parasites of North American voles except *H. horrida, H. costellatum* and *N. microti*.

*Hymenolepis horrida* (Text-figs. 1 & 2) and *Heligmosomum costellatum* (Text-figs. 3 & 4) are here recorded for the first time from North America, although they are known from various species of Eurasian voles. One of us (R. R.) has recovered these species from microtine rodents in Alaska, *H. horrida* occurring commonly in *Dicrostonyx, Lemmus, Microtus* and *Clethrionomys*, and *H. costellatum* in *Microtus*. It is suggested that these species are essentially

[1] This study was supported in part by grants-in-aid from the New York Zoological Society through its Jackson Hole Biological Station. The authors are indebted to Mr. Norman C. Negus and Mr. James Findley, of the Cleveland Museum of Natural History, who collected many of the hosts examined in connection with the present study and provided the data on host population densities. Dr. Jack D. Tiner kindly identified the species of *Syphacia* and *Trichuris*. The generous cooperation of Mr. James R. Simon, Director of the Jackson Hole Wildlife Park, greatly facilitated our work there.

[2] Department of Biological Sciences, Purdue University, and U. S. Public Health Service, Anchorage, Alaska.

arctic and subarctic in distribution in North America with southward extensions in the alpine zone of the Rocky Mountains.

The available descriptions of *Heligmosomum costellatum* are at variance, especially with regard to the interpretation of cuticular structures (Travassos & Darriba, 1929; Desportes, 1943). In view of the position which *H. costellatum* occupies as type of the genus on which the family Heligmosomidae Cram, 1927, is based, it seems desirable to supplement existing descriptions with the following observations based on abundant material from Wyoming voles. All measurements are in millimeters unless otherwise specified.

**Heligmosomum costellatum** (Dujardin, 1845). (Text-figs. 3 & 4).

Slender, rather small nematodes, with the characters of the genus; red in life, not spirally coiled. Cuticle with well-developed oblique longitudinal lines or ridges originating in the left lateral field and progressing obliquely posteriad to end in the right lateral field. Esophagus long, clavate and terminating in a short, slightly modified portion.

Male: body length 7.0-10.6, maximum width 0.125-0.152. Cephalic cuticular dilatation 0.069-0.10 long by 0.080-0.095 in diameter. Nerve ring 0.185-0.210, excretory pore 0.354-0.52 from the anterior extremity. Esophagus 0.4-0.5 long by 0.053-0.058 in maximum width. Cervical papillae apparently absent. Reproductive organs simple; testis originating 1.3-3.6 from the anterior extremity and narrowing to form a short vas deferens near the midpoint of the body. Seminal vesicle a slightly expanded portion of the genital tract narrowing gradually to form the ejaculatory duct. Pre-bursal papillae slender and very difficult to observe. Bursa large and slightly asymmetrical, the right lateral lobe being somewhat larger than the left. Ventral rays widely divergent, with a common stem; latero-ventral large and muscular. Lateral rays slender and with a common stem; the postero-lateral widely divergent from the group. Externo-dorsal rays long and slender, isolated at the point of origin. Dorsal ray originating near the bases of the externo-dorsals; small and difficult to observe, 0.050-0.056 long and branched to form two short, curved lateral rami and two longer, straight median rami. Dorsal lobe much reduced and difficult to observe. Genital cone with two slender papillae which encircle the protruded spicules. Spicules similar, slender, 0.01-0.013 in diameter at the proximal end, 0.85-0.99 long; each bifurcate 0.08-0.10 from the base to form two sub-equal processes, the longer ending in a diminutive hook. Gubernaculum apparently absent.

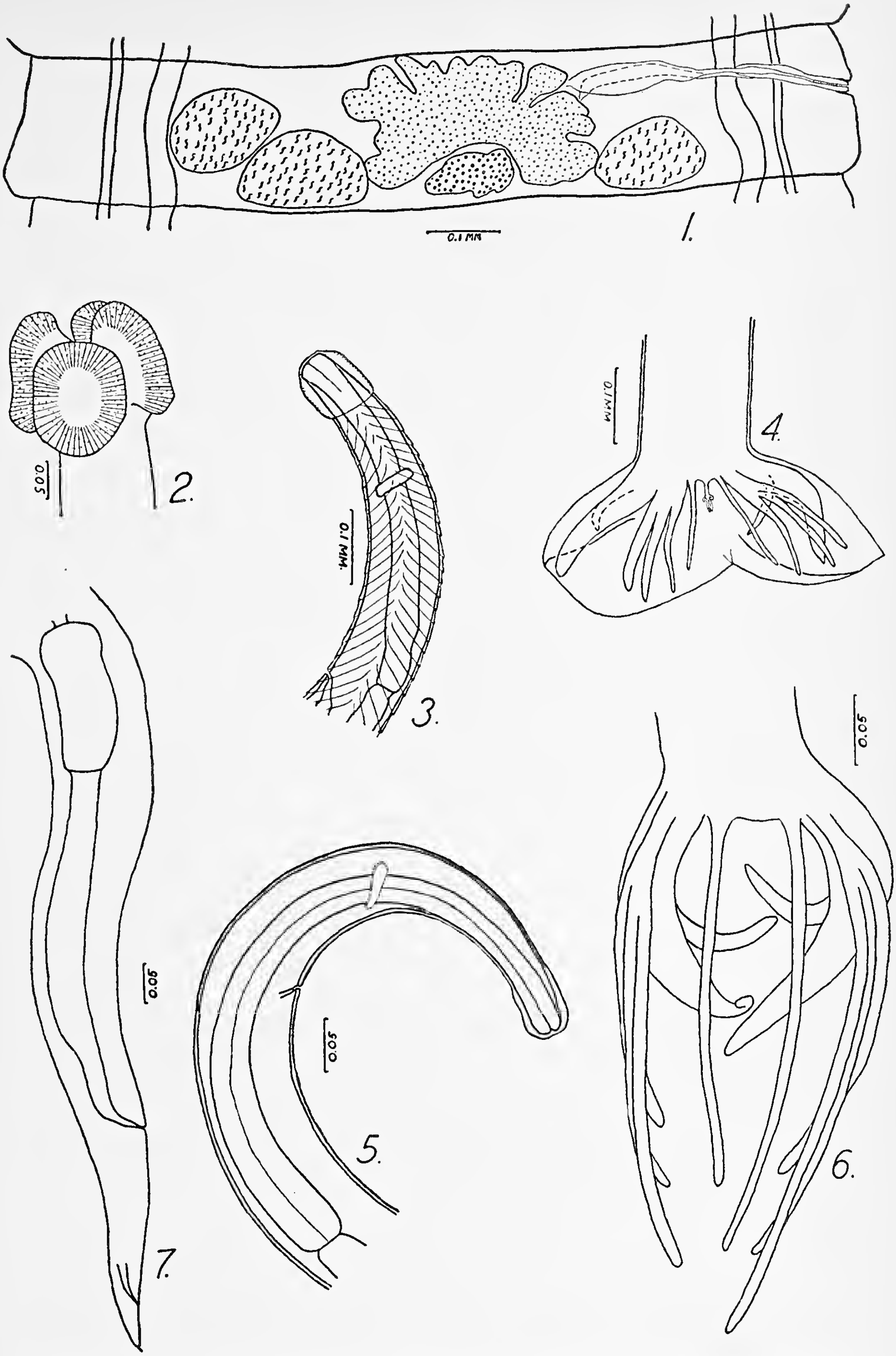
Female: body 8.5-15.0 long by 0.135-0.18 in maximum width. Cephalic cuticular dilatation 0.085-0.125 long by 0.083-0.098 in diameter. Nerve ring 0.175-0.225; excretory pore 0.35-0.51 from the anterior extremity. Esophagus 0.48-0.51 long by 0.055-0.06 in maximum width. Reproductive organs simple; ovary originating 3.5-5.0 from the anterior extremity, looping forward occasionally as it progresses posteriorly to form a short, indistinct oviduct joining the uterus about one-fourth the length from the posterior end. Ovejector well-developed; consisting of anterior, thick-walled infundibulum 0.16-0.21 in length, a sphincter and a posterior muscular ejectrix, lined with cuticle and 0.125-0.20 long; both sphincter and ejectrix with a prominent external layer of obliquely arranged muscle fibers. Vagina long, lined with cuticle and with an S-shaped portion near the midpoint. Vulva large, conspicuous, and located 0.32-0.48 from the posterior extremity. Tail 0.064-0.077 long, attenuated and terminated by a cuticular spine 0.012-0.015 in length. Eggs thin-shelled; 0.099-0.117 long by 0.049-0.053 wide. Embryos in the morula stage at the time of deposition.

Several nematodes recovered from voles in only the alpine zone of the Jackson Hole region appear to represent an undescribed species of *Nematospiroides* for which the name *N. microti* is proposed.

**Nematospiroides microti** n. sp. (Text-figs. 5-7).

Specific diagnosis: Small, spirally-coiled nematodes with the characters of the genus. Cuticle with minute transverse striations and 16 conspicuous longitudinal lines or ridges. Cephalic cuticular dilatation slightly asymmetrical. Cervical papillae not observed. Esophagus claviform. Reproductive organs simple.

Male: 5.8-6.0 long by 0.08-0.10 in maximum width. Cephalic cuticular dilatation measuring 0.052-0.065 in length by 0.038 in diameter. Diameter of head 0.027-0.028. Nerve ring 0.16-0.19 and excretory pore 0.30-0.34 from the anterior extremity. Esophagus 0.59-0.60 long, increasing in width from 0.024 anteriorly to a maximum of 0.045-0.053 near its junction with the intestine. Pre-bursal papillae apparently absent. Testis simple, originating about 0.15 posterior to the intestino-esophageal junction. Seminal vesicle short. narrowing to form ejaculatory duct about 2.25 from the posterior extremity. Bursa measuring 0.40-0.45 by 0.15-0.18 wide in the closed or folded position usually observed, asymmetrical. the right lateral lobe being larger than the left. Ventral rays widely divergent and with a common stem. Ventro-ventral small, slender, curving toward the mid-line to end 0.15-0.16 from the cloacal orifice. Lateral rays slender, elongate, parallel for most of their length, with a common stem and graduated in length; medio-lateral and postero-lateral rays divergent near the tips, the postero-lateral nearly attaining the bursal margin. Externo-dorsal rays slender, elongate and widely separated at the base. Dorsal ray 0.06-0.065 long, arising separately, and directed abruptly ventrad




TEXT-FIGS. 1-7. **1.** *Hymenolepis horrida*, mature proglottid. **2.** *Hymenolepis horrida*, scolex. **3.** *Heligmosomum costellatum*, anterior end. **4.** *Heligmosomum costellatum*, bursa copulatrix. **5.** *Nematospiroides microti* n. sp., anterior end. **6.** *Nematospiroides microti* n. sp., bursa copulatrix. **7.** *Nematospiroides microti* n. sp., posterior end of female.

toward the cloacal orifice where it branches to end in four slender points. Spicules simple, equal, filiform, 0.01 wide at the base and 2.08-2.20 in length; retracted portion enclosed in a well-developed, non-protrusible sheath. Gubernaculum apparently absent.

Female: 8.0-10.5 in length by 0.12-0.13 in maximum width. Cephalic cuticular dilatation 0.062-0.080 long by 0.046-0.048 in diameter. Diameter of head 0.032-0.035. Nerve ring located 0.20 and excretory pore 0.31 from anterior extremity. Esophagus 0.68-0.69 long by 0.05-0.062 in maximum width near the posterior end. Ovary originating 1.4-2.0 from the anterior end. Oviduct indistinct. Ovejector well developed, consisting of an anterior thick-walled infundibulum 0.16-0.19 long and a median sphincter which is fused with the muscular ejectrix to form an organ 0.17-0.18 in length. Vagina and ejectrix with a cuticular lining. Vulva located 0.28-0.32 from the posterior extremity. Tail 0.058-0.064 in length, attenuated, and terminating in a minute spine 0.01-0.012 in length. Eggs thin-shelled, 0.078-0.082 long by 0.04-0.043 in width. Embryo in early cleavage at the time of deposition.

Hosts: *Microtus montanus nanus* (type host) and *Microtus richardsoni macropus.*

Habitat: Small intestine.

Type locality: Brooks Mountain, Fremont County, Wyoming.

Holotype: Mature male, U. S. National Museum Helminthological Collection No. 46394.

Paratype: Mature female, U. S. National Museum Helminthological Collection No. 46394.

This species is readily distinguished from other members of the genus by the elongate lateral and externo-dorsal rays of the male.

The Jackson Hole region of Wyoming includes the valley of the Snake River from Yellowstone National Park on the north to the Hoback River on the south, and from the continental divide west to the Grand Teton Range. The valley slopes from about 7,000 feet above sea level in the north to 6,000 feet in the south, and has an area of about 337 square miles. Voles of the genus *Microtus* were found in six rather well defined habitats within this general area. The habitats are discussed separately.

**Habitat I: Sage flats.** Altitude 6,500 feet. Host population density about 1.0 vole per acre. A considerable portion of the valley floor between the towns of Moran and Jackson is covered by a moderately dense growth of sagebrush (*Artemesia* spp; mainly *A. tridentata* Nutt.). According to the classification of Merriam, this is the only habitat in the Jackson Hole region characteristic of the transition life zone. One of the quadrats located in this habitat (5 miles south of Moran) yielded only two specimens of *Microtus montanus nanus,* both of which were negative for helminth parasites. Although this represented an inadequate sample, it is believed that the degree of parasitism in this habitat must be very low.

**Habitat II: Aspen consocies.** Altitude 6,700 feet. Host population density about 3.5 voles per acre. This vegetation type (*Populus tremuloides* Michx.) occurs in several small, relatively dry areas within the Wildlife Park and forms a part of the broad ecotone between the lower limits of the Canadian and the upper limits of the transition life zone. *Microtus longicaudus mordax* was collected only in this habitat. Two of five individuals were parasitized, one with a single specimen of *Paranoplocephala infrequens* and another with two of *Syphacia obvelata.* One of three specimens of *M. montanus nanus* taken from this habitat harbored 23 *S. obvelata* in the cecum.

**Habitat III: Dry meadow.** Altitude 6,700 to 7,000 feet. Host population density moderate (estimated at 10 per acre). Several areas in the vicinity of the Wildlife Park supported a rather dense growth of medium-height grasses and herbaceous plants. This habitat is classified in the transition-Canadian ecotone. Because of the drainage or topography, this habitat is too dry to support the sedges and willows of adjacent lowland areas. Collections were made near Two-ocean Lake, Emma Matilda Lake, and Elk Ranch. Twenty-two specimens of *Microtus montanus nanus* from this habitat were parasitized by the following helminths: *Andrya primordialis* (18 per cent.); *Paranoplocephala infrequens* (18 per cent.); *P. borealis* (5 per cent.); *P. variabilis* (5 per cent.); *Syphacia obvelata* (9 per cent.). Fourteen (64 per cent.) of these animals were negative for helminths.

**Habitat IV: Willows and wet meadows.** Altitude 6,700 feet. Host population density moderate (about 15 per acre). Wet or swampy areas in the transition-Canadian ecotone were common in the vicinity of streams in the Park, and are characterized by a dense growth of willows (*Salix* spp.) interspersed with open meadows of grasses and sedges. *Microtus pennsylvanicus modestus* was found only in this habitat, as was the trematode *Quinqueserialis hassalli.* The latter is presumably limited by the distribution of the snail intermediate host. The incidence of infection of voles in this habitat is summarized in Table I.

**Habitat V: Sub-alpine meadow.** Altitude 9,200 feet. Host population density high (estimated at 40 per acre). Two species of *Microtus* (*M. richardsoni macropus* and *M. montanus nanus*) were collected in the moist, park-like openings along small streams in the spruce-fir (*Picea parryana-Abies* sp.) climax forest of the Canadian life zone. Two areas near Togwotee Pass, Fremont County, Wyoming, were selected for study, and ten specimens of *M. richardsoni macropus* collected there were parasitized by helminths as follows: *Andrya primordialis* (30 per cent.); *A. macrocephala* (10 per cent.); *Trichuris opaca* (20 per cent.). Two voles were

not infected by helminths. *Microtus montanus* also occurred in this habitat, but no examinations were made of this species.

**Habitat VI: Alpine meadow.** Altitude 11,000 feet. Host population density about 61 voles per acre. Large areas of flat or gently sloping meadow covered the tops of some of the mountains at the eastern margin of the region under consideration. These meadows were usually 1,000 feet or more above timberline and were covered with deep snow during most of the year. The vegetative cover was low but very dense. The alpine buttercup (*Ranunculus* sp.) and a species of *Mertensia* were characteristic of this habitat. The top of Brooks Mountain, Fremont County, Wyoming, was selected for study because of its accessibility. Eighty-one per cent. of 21 *Microtus montanus nanus* and 60 per cent. of 10 *M. richardsoni macropus* collected in this habitat were infected with the helminths listed in Table II. Two cestodes and one nematode from these hosts were damaged and specific determination was not possible. These are listed in Table II as *Andrya* sp., *Paranoplocephala* sp. and *Nematospiroides* sp.

## Discussion.

The habitats included in this study were unusually varied, ranging from the hot, dry sage flats to areas of swamp or perennial snow. Since they were concentrated in an area less than 35 miles in diameter, an excellent opportunity was afforded for an ecological investigation in relation to helminth parasites.

One species of vole (*Microtus montanus nanus*) was found to range throughout the region and was absent only from the coniferous forests where the small, succulent forms of vegetation, apparently required as a food supply, were lacking. The three other species of voles collected during the course of this study apparently were much more demanding in their habitat requirements. *Microtus pennsylvanicus modestus* was observed to be restricted to swampy areas supporting dense growths of sedges and willows (Habitat IV). *Microtus longicaudus mordax* was found only in the open groves of aspen (Habitat II). The large water-vole, *Microtus richardsoni macropus*, was apparently restricted to the subalpine meadows occurring along streams in the spruce-fir forests at high altitudes (Habitat V) and to the alpine meadows occurring above timber-line (Habitat VI).

This unique pattern in the distribution of four species of the same genus of voles offered an opportunity for the evaluation of host specificity as opposed to ecological factors in regard to the geographic distribution of certain parasites. The parasites encountered in any one habitat showed neither preference for *M. montanus nanus*, the only vole occurring in all habitats studied, nor for any other species of vole limited to a single specific habitat (see Tables I and II). The examination of Table III shows that some helminths were generally distributed, while others were restricted in their distribution. Since host specificity does not explain this pattern of parasite distribution, other factors must be considered.

Host population density may influence the distribution and incidence of infection by these helminths. Although the greatest numbers of parasites, both qualitative and quantitative, occurred in habitats where host density was greatest, it seems unlikely that host density is the only factor involved.

The distribution patterns of some of the parasites encountered appear to be more understandable when their life cycles are taken into consideration. Although the intermediate host of *Quinqueserialis hassalli* has not been determined, it is presumably a gastropod mollusc. Herber (1942) reported a snail, *Gyraulus parvus* (Say), as the intermediate host of *Q. quinqueserialis* (Barker & Laughlin, 1911), a species closely related to the one with which we are concerned. This species develops through a sporocyst and two redial generations in the snail, and the

TABLE I.

Incidence of Parasitism for Voles Collected in Habitat IV (Wet Meadows).

| | *Microtus pennsylvanicus modestus* | *Microtus montanus nanus* | Total for Habitat IV |
|---|---|---|---|
| Number of hosts examined | 15 | 14 | 29 |
| *Quinqueserialis hassalli* | 20% | 7% | 14% |
| *Andrya primordialis* | 13% | 14% | 14% |
| *Andrya macrocephala* | 13% | 21% | 17% |
| *Paranoplocephala infrequens* | 33% | 29% | 31% |
| *Syphacia obvelata* | 20% | 14% | 17% |
| % of hosts infected with one or more of the above species | 60 | 64 | 62 |

emerging cercariae encyst on aquatic vegetation. Assuming a similar life cycle for *Q. hassalli*, only those voles which include a suitable habitat for the intermediate host within their home range would be exposed to infection. The apparent limitation of *Q. hassalli* to one habitat would support this.

If it can be assumed that mites serve as the intermediate host for the anoplocephaline cestodes encountered, the distribution of mites would determine the occurrence of such cestodes. This has been more completely discussed in a previous paper (Rausch & Tiner, 1949).

All nematodes collected in connection with the present study are assumed to have direct life cycles. If this is true, the distribution and abundance of susceptible hosts, coupled with conditions favorable to the survival of infective eggs and larvae, would strongly influence the occurrence of such parasites. The life cycle of *Hymenolepis horrida* is unknown.

Four species, viz., *Hymenolepis horrida*, *Heligmosomum costellatum*, *Nematospiroides microti* and *Trichuris opaca*, were restricted to highland habitats (V and VI). Since both of these habitats are near or above timber line (9,200 to 11,000 feet) they are characterized by prolonged winter conditions of deep snow, low temperature and high winds. Extensive snow drifts were observed in the alpine habitat during the first week of July. The densest populations of both hosts and parasites were encountered in these habitats. The permanent dampness and coolness here would perhaps account for better survival of nematode eggs and larvae, and also contribute to a luxuriant growth of vegetation upon which the voles are dependent for food. Previous work (Rausch & Tiner, 1949) would indicate that moisture is of great importance in connection with degree of abundance of vole parasites. This is true from both a qualitative and quantitative standpoint.

A suitable explanation for the restriction of four species of parasites to highland habitats appears to be lacking. It is noteworthy that *Hymenolepis horrida* and *Heligmosomum costellatum* are European parasites, not previously recorded from North America. Their occurrence only in the highland habitats in the Jackson Hole region and near sea level in Alaska may be of zoogeographic significance, but further study is necessary to allow any definite conclusions.

## Summary.

An ecological and taxonomic study of the helminth parasites of voles (*Microtus* spp.) in the Jackson Hole region of Wyoming is reported.

*Nematospiroides microti* n. sp. from *Microtus montanus nanus* and *M. richardsoni macropus* is described and figured

A cestode, *Paranoplocephala infrequens*, and a nematode, *Syphacia obvelata*, were generally distributed throughout the region in all habitats except the sage flats.

A trematode, *Quinqueserialis hassalli*, was recovered only from voles collected near streams at low altitudes. This was presumably due to the localized distribution of the molluscan intermediate host.

Four helminths, viz., *Hymenolepis horrida*, *Heligmosomum costellatum*, *Nematospiroides microti* and *Trichuris opaca*, were restricted in their distribution to the alpine and sub-alpine meadows. Of these parasites, *H. horrida* and *H. costellatum* are reported for the first time from North America. Most of the other host and locality records are new.

TABLE II.

Incidence of Parasitism for Voles Collected in Habitat VI (Alpine Meadow).

| | *Microtus montanus nanus* | *Microtus richardsoni macropus* | Total for Habitat VI |
|---|---|---|---|
| Number of hosts examined | 21 | 10 | 31 |
| *Andrya primordialis* | 29% | 20% | 26% |
| *Andrya macrocephala* | 5% | 20% | 10% |
| *Andrya* sp. | 0 | 10% | 3% |
| *Paranoplocephala infrequens* | 29% | 20% | 26% |
| *Hymenolepis horrida* | 10% | 20% | 13% |
| *Heligmosomum costellatum* | 24% | 40% | 29% |
| *Nematospiroides microti* n. sp. | 10% | 10% | 10% |
| *Nematospiroides* sp. | 0 | 10% | 3% |
| *Syphacia obvelata* | 48% | 30% | 42% |
| % of hosts infected with one or more of the above species | 81 | 60 | 74 |

TABLE III.

Helminth Parasites of Voles from Various Habitats in the Jackson Hole Region of Wyoming.

| | Sage Flats | Aspen Groves | Dry Meadow | Willows & Wet Meadows | Sub-alpine Meadow | Alpine Meadow | Total for Region |
|---|---|---|---|---|---|---|---|
| Altitude in feet | 6,500 | 6,700 | 6,700 | 6,700 | 9,200 | 11,000 | — |
| Vole Population / acre | 1 | 7 | 10* | 15 | 40* | 61 | — |
| No. of vole species present | 1 | 2 | 1 | 2 | 2 | 2 | 4 |
| No. of voles examined | 2 | 5 | 22 | 29 | 10 | 31 | 103 |
| *Syphacia obvelata* | 0 | 14% | 9% | 17% | 30% | 42% | 24% |
| *Paranoplocephala infrequens* | 0 | 14% | 18% | 31% | 30% | 26% | 25% |
| *Andrya primordialis* | 0 | 0 | 18% | 14% | 30% | 26% | 19% |
| *Andrya macrocephala* | 0 | 0 | 0 | 17% | 10% | 10% | 9% |
| *Hymenolepis horrida* | 0 | 0 | 0 | 0 | 30% | 13% | 7% |
| *Heligmosomum costellatum* | 0 | 0 | 0 | 0 | 10% | 29% | 10% |
| *Paranoplocephala variabilis* | 0 | 0 | 5% | 0 | 0 | 0 | 2% |
| *Paranoplocephala borealis* | 0 | 0 | 5% | 0 | 0 | 0 | 2% |
| *Quinqueserialis hassalli* | 0 | 0 | 0 | 14% | 0 | 0 | 4% |
| *Trichuris opaca* | 0 | 0 | 0 | 0 | 20% | 0 | 2% |
| *Nematospiroides microti* | 0 | 0 | 0 | 0 | 0 | 10% | 3% |
| % of hosts infected with one or more of the above species | 0 | 28 | 36 | 62 | 80 | 74 | 60 |

* Estimated.

Available data indicate that host specificity was not a factor in restricting the distribution of parasites.

Although the greatest numbers of parasites, both qualitative and quantitative, occurred in habitats where host density was greatest, it seems unlikely that host density is the only factor involved.

## Bibliography.


Bole, B. P., Jr.

1939. The quadrat method of studying small mammal populations. *Cleveland Mus. Nat. Hist., Sci. Publ.*, 5 (4): 15-77.

Desportes, C.

1943. Un curieux nematode, *Heligmosomum costellatum* (Dujardin, 1845). *Ann. Parasit.*, 19: 161-167.

Elton, C., E. B. Ford, J. R. Baker & A. D. Gardner

1931. The health and parasites of a wild mouse population. *Proc. Zool. Soc. London*, 1931, pp. 657-721.

Harkema, R.

1936. The parasites of some North Carolina rodents. *Ecol. Monogr.*, 6: 2-153.

Herber, E. C.

1942. Life history studies on two trematodes of the sub-family Notocotylinae. *Jour. Parasit.*, 28: 179-196.

Kirschenblatt, J. D.

1938. Die Gesetzmässigkeiten der Dynamik der Parasitenfauna bei den mäuseähnlichen Nagetieren (Muriden) in Transkaukasien. Diss. (Univ. Leningrad), pp. 5-92.

Rankin, J. S.

1945. Ecology of the helminth parasites of small mammals collected from Northrup Canyon, Upper Grand Coulee, Wash. *Murrelet*, 26: 11-14.

Rausch, R. & J. D. Tiner

1948. Studies on the parasitic helminths of the north central states. I. Helminths of Sciuridae. *Amer. Midl. Nat.*, 39 (3): 728-747.

1949. Studies on the parasitic helminths of the north central states. II. Helminths of voles (*Microtus* spp.)—preliminary report. *Amer. Midl. Nat.*, 41 (3): 665-694.

Travassos, L. & A. Darriba

1929. Notas sobre Heligmosominae. *Sc. Med.*, 7: 432-438.

# 16.

# Migration of Pieridae (Butterflies) Through Portachuelo Pass, Rancho Grande, North-central Venezuela.[1]

William Beebe.

*Director, Department of Tropical Research, New York Zoological Society.*

(Plate I).

[This is one of a series of papers resulting from the 45th, 46th and 47th Expeditions of the Department of Tropical Research of the New York Zoological Society, made during 1945, 1946 and 1948, under the direction of Dr. William Beebe, with headquarters at Rancho Grande in the National Park of Aragua, Venezuela. The expeditions were made possible through the generous cooperation of the National Government of Venezuela and of the Creole Petroleum Corporation.

[The characteristics of the research area are in brief as follows: Rancho Grande is located in north-central Venezuela (10° 21′ N. Lat., 67° 41′ W. Long.), 80 kilometers west of Caracas, at an elevation of 1,100 meters in the undisturbed montane rain forest which covers this part of the Caribbean range of the Andes. The migration flyway of Portachuelo Pass, which is also the water-shed between the Caribbean and Lake Valencia, is 200 meters from Rancho Grande. Adjacent ecological zones include seasonal forest, savanna, thorn woodland, cactus scrub, the fresh-water lake of Valencia and various marine littoral zones. The Rancho Grande area is generally subtropical, being uniformly cool and damp throughout the year because of the prevalence of the mountain cloud cap. The dry season extends from January into April. The average humidity during the expeditions, including parts of both wet and dry seasons, was 92.4%; the average temperature during the same period was 18° C.; the average annual rainfall over a five-year period was 174 cm. The flora is marked by an abundance of mosses, ferns and epiphytes of many kinds, as well as a few gigantic trees. For further details see Beebe & Crane, *Zoologica*, Vol. 32, No. 5, 1947. Unless otherwise stated, the specimens discussed in the present paper were taken in the montane cloud forest zone, within a radius of one kilometer of Rancho Grande.

[For an account of Portachuelo Pass, together with a general introduction to the groups of migrating insects and migrational factors, see "Insect Migration at Rancho Grande," by William Beebe, *Zoologica*, 1949, Vol. 34, No. 12, pp. 107-110; for preceding papers in this series see, "Migration of Papilionidae," *ibid*, 1949, Vol. 34, No. 14, pp. 119-126, and "Migration of Danaidae, Ithomiidae, Acraeidae and Heliconidae," *ibid*, 1950, Vol. 35, No. 3, pp. 57-68.]

## Migration of Pieridae.

Among the migrants through Portachuelo Pass this family is represented by 18 genera and 44 species. Among them are a few of the most abundant migrants, passing day after day and month upon month in uncountable numbers. Many are so similar in size, pattern and coloration that in field identification they can only be lumped, and dependence can be placed solely on captured specimens. Others are clearly distinguishable as far as the lenses of binoculars will detect them, either far down the gorge or high in air.

We frequently found an unexpectedly large concentration of species mingled in large, dense, swiftly flying flocks of individual pierids. The following will illustrate this: In 1948, April 27, took 8 specimens of 5 species; May 23, 18 specimens of 14 species; June 6, 35 specimens of 13 species; July 3, 6 specimens of 5 species; July 5, 11 specimens of 10 species; July 8, 20 specimens of 11 species.

We had few opportunities of tracing the Rancho Grande migration of Pieridae any considerable distance north or south of Portachuelo Pass. The following were taken, among others, which flew on board the *Santa Paula* on August 8, 1948, while we were steaming close in shore westward from Puerto Cabello. The insects were headed eastward: *Ascia m. monuste* (males and females), *Anteos maerula*, *Eurema albula*, *salome* and *venusta*.

### Dismorphinae.

The subfamily Dismorphinae is represented by two genera and eight species. The genus *Dismorphia* includes seven of these species which defy any color classification, utterly confusing in the variety of their patterns and coloring, both specifically and sexually. Superficially, on the wing, these butterflies might be mistaken for ithomiids, acraeids, heliconids and even one or two day-flying moths with which they were associated as they poured through the Pass. None can be said to be abundant although occasional small flocks were seen. Three species are represented by single specimens.

**Dismorphia amphione astynomides** Rober.

*Field Name*: Many-colored Pierid.

*Species Range*: Mexico to Boliva and Guiana.

*Subspecies Range*: Venezuela and Trinidad.

*Field Characters*: The male has a typical

[1] Contribution No. 881, Department of Tropical Research, New York Zoological Society.

ithomiine pattern on exposed portions, but pierid white on concealed anterior parts of hindwings. In flight the white flashes out.

*Number*: Total recorded, 36. Taken, 1.

*Sex*: Males only taken and seen.

*Date*: June 5, 6 and 7.

*Frequency*: Observed on only three days in June.

*Record*: 1948—June 5 (3 clearly seen but out of reach), 6 (27 seen and 1 caught, No. 48747), 7 (7 passed beyond reach in a dense swarm of *Eurema*).

**Dismorphia critomedia** (Geyer).

*Field Name*: Black-and-white Round-winged Dismorphia.

*Species Range*: Panama to Peru and Brazil.

*Field Characters*: Forewing black with white oblique band and two dots; hindwing white, black bordered. Hardly to be distinguished from *Leptophobia pentheca* and from female *Dismorphia nemesis*.

*Number*: Total, 7. Taken, 7.

*Sex*: Both sexes taken.

*Date*: April 23 to June 11.

*Frequency*: None recognized except those taken.

*Non-migrant Record*: A second male taken on June 11 was on Water Trail, some distance from the Pass, and loitering. In 1945 two females were taken in the jungle on July 1 and August 4, well away from the Pass.

*Record*: 1948—April 23 (1), 27 (male, No. 48412); May 21 (male), 23 (male); June 6 (male), 10 (female, No. 48558), 11 (male).

**Dismorphia hyposticta** (Felder).

*Field Name*: Black-bordered Yellow-winged Dismorphia.

*Species Range*: Colombia and Venezuela.

*Field Characters*: Similar to *D. medora* but with narrower black border to hindwings. Close to *D. critomedia* but with white replaced by yellow.

*Number*: Total seen, 8. Taken, 4.

*Sex*: Both sexes taken.

*Date*: May 9 to July 3.

*Frequency*: Probably many more seen but not recognized with certainty.

*Record*: 1948—May 9 (female, No. 48513), 23 (female): June 6 (1); July 3 (1, No. 48725).

**Dismorphia medora medora** (Doubl.).

*Field Name*: Broad-bordered Yellow Dismorphia.

*Species Range*: Panama to Peru.

*Subspecies Range*: Colombia and Venezuela.

*Field Characters*: Indistinguishable from *D. hyposticta* except for a much wider black margin to the hindwings. This character is evident on the wing when individuals are flying slowly and near at hand. At a distance often confused with a yellow and black day-flying moth, the two species mingling in the same flock on days of heavy migration.

*Number*: Total, 127. Taken, 12.

*Sex*: Both sexes taken.

*Date*: April 23 to September 8.

*Frequency*: Taken singly, but nearly 100 seen on July 8.

*Non-migrants*: In 1945, 2 were taken in the jungle, a female on July 16 and a male on the 20th.

*Record*: 1946 — August 7 (male, No. 46903). 1948—April 23 (male); May 1 (female, No. 48438), 25 (male and female), 26 (female), 31 (male); June 6 (male); July 6 (19 seen), 8 (female taken, 96 seen, in company with day-flying moths), 27 (male taken, several seen); September 8 (male and female).

**Dismorphia melite** (Linn.).

*Field Name*: Black-tipped Yellow Dismorphia.

*Species Range*: Mexico to Southern Brazil.

*Field Characters*: A rare, pale green pierid, with black tips and foredge spot on forewings.

*Number*: Taken, 1.

*Record*: 1946—May 13 (1 taken).

**Dismorphia nemesis nemesis** (Latr.).

*Field Name*: Pointed-wing Dismorphia.

*Species Range*: Costa Rica to Colombia and Bolivia.

*Subspecies Range*: Colombia and Venezuela.

*Field Characters*: Sexually dimorphic. Male forewing black with fine white streaks, hindwing shining gray, posteriorly yellow. Female with curved and pointed forewing, close to *D. critomedia*.

*Number*: Total, upwards of 600. Taken, 28.

*Sex*: Both sexes taken.

*Date*: April 27 to August 2.

*Frequency*: The most abundant of this subfamily. The sexes often segregated, as 63 females on June 10, and 115 males on June 24.

*Non-migrants*: In 1945 a male was taken in the jungle, and a female in the adjoining Pass of Choroni.

*Record*: 1946—May 28 (female). 1948—April 27 (2 females taken, No. 48409, 150 plus seen); May 8 (female), 21 (2 females), 26 (male, No. 48627), 29 (male); June 6 (5 males, 3 females taken. 200 plus seen), 10 (female taken, 63 females seen), 24 (2 males taken, 115 males seen); July 2 (female), 8 (female, No. 481121), 14 (2 females), 15 (female), 16 (2 males), 26 (female); August 2 (male).

**Dismorphia theucharila theucharila** (Doubl.).

*Field Name*: Small Many-colored Dismorphia.

*Species Range*: Venezuela and Colombia.

*Subspecies Range*: Venezuela.

*Field Characters*: A small, rare ithomiid mimic.

*Number*: A single, worn specimen taken.

*Record*: 1946—June 1 (1 taken).

The second genus of this subfamily is represented among the migrants by a single species.

**Pseudopieris nehemia virdula** (Feld.).

*Field Name*: Small Pale Greenish Pierid.

*Species Range*: Mexico to South Brazil.

*Subspecies Range*: Colombia and Venezuela.

*Field Characters*: A medium, delicate pierid, bluish white, unmarked.

*Number*: Total, 22. Taken, 2.

*Date*: May 23 and 29.

*Frequency*: A flurry of 21 individuals in a single flock on May 23, and a single one taken on the 29th, were all that were recorded.

*Record*: 1948—May 23 (1 taken, 21 seen), 29 (1 taken).

The pierid Tribe Euchlorini is represented among the migrants by a single genus and species.

**Hesperocharis marchalii marchalii** (Guérin).

*Field Name*: Dark-veined White.

*Species Range*: West side of South America from Colombia to Argentina.

*Subspecies Range*: Colombia and Venezuela.

*Field Characters*: Although only two specimens were taken, I certainly identified this species several times from its unique dark veining, especially strong on the ventral side. Otherwise it was just another medium White.

*Number*: Total, 7. Taken, 2.

*Date*: 1948—May 29 (1, No. 48669); July 21 (1, No. 481271), 24 (3 seen), 26 (1 seen), 27 (1 seen).

Three species of *Catasticta* and two of *Leodonta* are included among the migrants, and may be considered in a loose color group. In spite of apparently good pattern characters I have no sight records for any species. All seem rare.

**Catasticta crowleyi** Butler.

*Field Name*: Blackish-brown Pierid.

*Species Range*: Venezuela.

*Field Characters*: The only migrant pierid which is in general blackish-brown, obscurely dotted with white. Hints of red and yellow spotting below.

*Number*: Taken, 6.

*Date*: April 27 to August 2.

*Record*: 1946 — August 2 (No. 46880). 1948—April 27 (No. 48408); May 25 (1), 29 (1); July 14 (1), 15 (1).

**Catasticta flisa flisa** (Herrich-Schaeffer).

*Field Name*: White-V Pierid.

*Species Range*: Central America to Peru.

*Subspecies Range*: Colombia, Ecuador and Venezuela.

*Field Characters*: White-dotted black except for an elongated white V or wedge in wing centers.

*Numbers*: Taken, 3.

*Sex*: Both sexes taken.

*Date*: April 29 to July 21.

*Record*: 1948 — April 29 (female, No. 491447); May 6 (1); July 21 (male).

**Catasticta prioneris albescens** Rober.

*Field Name*: White-dotted-border, Yellow-underside.

*Species Range*: Colombia and Peru.

*Subspecies Range*: Western Colombia and Venezuela.

*Field Characters*: White, with broad, white-spotted black border. Easily confused with *Pieris mandela*, but none were recognized on the wing. Yellow spots underwing.

*Number*: Taken, 6.

*Date*: April 29 to September 7.

*Record*: 1946—September 7 (No. 461156). 1948—April 29 (1); May 1 (1), 9 (1); June 6 (1); July 6 (1).

**Leodonta dysoni dysoni** Doubl.

*Field Name*: Yellow-spotted Underwing.

*Species Range*: Costa Rica to Peru.

*Subspecies Range*: Venezuela.

*Field Characters*: Larger, and with wider border, but very close in pattern to *Catasticta prioneris albescens*.

*Number*: A single specimen taken.

*Record*: 1948—July 2 (1).

**Leodonta tagasta marginata** Scho.

*Field Name*: Yellow-and-Red-spotted Underwing.

*Species Range*: Venezuela, Ecuador and Peru.

*Subspecies Range*: Venezuela.

*Field Characters*: The large yellowish underwing spots distinguish this species. Above close to *Pieris mandela*.

*Number*: Taken, 5.

*Date*: April 8 to July 17.

*Record*: 1945 — April 8. 1948 — May 21 (1); July 2 (1), 14 (1), 17 (1).

**Archonias tereas critias** (Feld.).

*Field Name*: Papilio-mimic Pierid.

*Species Range*: Mexico to South Brazil and Ecuador.

*Subspecies Range*: Colombia and Venezuela.

*Field Characters*: A startling mimic of the male *Papilio anchises osyris*, scarcely to be differentiated in the hand. Still more remarkable is the fact that in size and pattern the sexes of *Archonias* differ in exactly the same way as do the corresponding sexes of the *Papilio* model. This includes greater size, large extent of white and scarlet spots in the females of both species. The pierids can be told, in the hand, by the inconspicuous line of submarginal white dots on the under side of the hindwings.

*Number*: Many probably seen but confused with Papilios.

*Sex*: Both sexes taken.

*Date*: April 8 to July 18.

*Frequency*: Unlike any other species of migrant, while a number were taken in 1945 and considerably more in 1946, not a single individual was either seen or taken in the year 1948.

*Non-migrants*: In 1945 six males were taken along jungle trails on June 1, 8 (8), 14

and 20 (2). In addition a female was captured in Limon on July 3.

*Record*: 1946—April 8, 10, 12, 13 and 27; May 4, 12 (female); June 28, 30 (male and female); July 1, 5, 9, 18.

**Charonias eurytele caraca** Kaye.

*Field Name*: Small Ithomiid Mimic.

*Species Range*: Guatemala to Colombia and Ecuador.

*Subspecies Range*: Venezuela.

*Field Characters*: Too close to several species of ithomiids to distinguish usually with certainty on the wing, although it has considerably less black than any of the other family.

*Number*: Total, 22. Taken, 4.

*Date*: April 29 and 30.

*Record*: 1948—April 29 (1, No. 48661), 30 (3 taken, No. 48459, 18 seen. I base this sight record on the fact that the 3 taken were from a small, dense flock of 18 others).

**Pyrrhybris pyrrha malenka** Hew.

*Field Name*: Large Ithomiid Mimic.

*Species Range*: Central America to South Brazil.

*Subspecies Range*: Venezuela and Colombia.

*Field Characters*: Larger than *Charonias*. Indistinguishable on the wing from the ithomiid *Tithorea harmonia furia*, and *Heliconius metalilis*.

*Number*: Only 2 seen and taken.

*Record*: 1946—September 8 (female, No. 461175). 1948 — June 24 (1, No. 48895); July 11 (1 taken at Kilometer 30, north of the Pass, No. 481148).

**Pereute charops meridana** Fruh.

*Field Name*: Melpomene Mimic.

*Species Range*: Guatemala to Ecuador and Colombia.

*Subspecies Range*: Venezuela.

*Field Characters*: The female above and below, and the male below, are startlingly like the scarlet and black of *Heliconius melpomene*. The male above is a dusty black. This pattern closely resembles that of the nymphalid *Adelpha lara*, but the latter has a swift direct flight.

*Number*: Total, 79. Taken, 24.

*Sex*: Both sexes taken.

*Date*: April 1 to September 8.

*Frequency*: This species migrates singly or in small flocks, the sexes usually being segregated in the latter case. The total count showed 32 males and 47 females. A number of times this species was found flying with its model, *Heliconius melpomene*.

*Flight*: Like the flight of the *Heliconius* model, this species had a wavering, low and apparently weak flight.

*Variations*: In the male taken July 21 the ventral red shows faintly on the upper side, known as variety *cauca* Rober. In males taken on April 1, May 1, June 6 and July 16 and 20, the ventral red is replaced by bright yellow.

*Record*: 1945—June 24 (female); August 4 (female). 1946 — April 29 (male); September 7 (female). 1948—April 1 (1 male, 3 females), 26 (female, No. 48450a, 8 others seen), 29 (female), 30 (3 females taken, No. 48450, 18 others seen; 2 males taken, No. 48459, 11 others seen); May 1 (male), 5 (12 males seen), 25 (female, No. 48460, 7 seen); June 6 (male); July 16 (male and female), 20 (male and female), 21 (male).

The Tribe Pierini is represented by six genera. These may be superficially defined as medium sized Whites, tipped or bordered with black. *Melete* is the only one appreciably greenish.

**Leptophobia aripa aripa** (Bois.).

*Field Name*: Medium Notch-border White.

*Species Range*: Mexico to Brazil and Bolivia.

*Subspecies Range*: Colombia and Venezuela.

*Field Characters*: Forewing black bordered with notch. Plain white hindwing distinguishes it from *tovaria* and the two species of *Itaballia*.

*Number*: Rare among the migrants. Taken, 5.

*Sex*: Both sexes taken.

*Date*: April 27 to October 7.

*Record*: 1945—June 20 (1). 1946: October 7 (1). 1948—April 27 (1, No. 48410), 30 (1); May 9 (2); July 2 (1).

**Leptophobia tovaria tovaria** (Feld.).

*Field Name*: Broad-bordered White.

*Species Range*: Colombia and Venezuela to Peru.

*Subspecies Range*: Colombia and Venezuela.

*Field Characters*: Very wide-bordered notched white. Dark-veined below. Easily confused with *L. penthica* and *Pieris mandela*.

*Number*: A rare insect. Taken, 5.

*Sex*: Both sexes taken.

*Date*: April 29 to September 7.

*Record*: 1946 — September 7 (1 taken). 1948—April 29 (1); May 28 (1); June 6 (1); July 15 (1). Each insect thus taken in a different month.

**Leptophobia penthica stamnata** (Lucas).

*Field Name*: Broad-bordered Spot White.

*Species Range*: Venezuela and Colombia to Peru.

*Subspecies Range*: Venezuela.

*Field Characters*: The black border reaches to the central white and cuts off a large forewing spot. Confused only with dark colored *Pieris mandela*.

*Number*: Rare. Only 3 taken.

*Sex*: Both sexes taken.

*Date*: May 8 to July 3.

*Record*: 1948—May 8 (1, No. 48500), 15 (1); July 3 (1).

**Melete lycimnia eurymnia** (Feld.).

*Field Name*: Large Black-bordered Green.

*Species Range*: Colombia, Venezuela and Brazil.

*Subspecies Range*: Colombia and Venezuela.

*Field Characters*: The only large greenish pierid with a wide border and a rectangular spot on the fore-edge of the forewing.

*Number*: Only 2 specimens taken.

*Date*: May 28 to July 21.

*Record*: 1946—May 28 (1). 1948—July 21 (1, No. 481277).

**Andropodum drusilla drusilla** (Cramer).

*Field Name*: Medium Faint-tipped White (male); Black bordered-and-edged White (female).

*Species Range*: South Florida to Brazil.

*Subspecies Range*: Colombia and Venezuela.

*Field Characters*: Male white with a faint gray wing tip; female black-bordered.

*Number*: Taken, 18.

*Sex*: Both sexes taken.

*Date*: April 28 to July 21.

*Record*: 1946—April 28 (male); May 25 (1). 1948—May 25 (female); June 6 (female, No. 48734), 15 (3 males, No. 48794); July 5 (male, No. 481086), 8 (6 females), 13 (male), 17 (2 females), 21 (2 males).

**Ascia monuste monuste** (Linn.).

*Field Name*: Scallop-bordered Medium White.

*Species Range*: Southern United States and West Indies to Venezuela and Argentina.

*Subspecies Range*: Central America to Venezuela and Argentina.

*Field Characters*: The scalloped black border on all wings identifies this species even on the wing.

*Number*: Several thousand seen. Taken, 60.

*Sex*: Both sexes taken.

*Date*: April 15 to September 1.

*Record*: 1946—May 23 (1), 28 (3 taken); September 1 (55 counted). 1948—April 15 (150 counted); June 6 (3 taken, No. 48736); July 5 (1, No. 481089), 8 (5), 10 (1 taken, 100's seen), 13 (2 taken, 100's seen), 15 (13), 16 (6), 17 (1), 20 (3), 21 (14), 26 (7 taken, 1000's passing), 29 (800 counted); August 2 (2).

**Ascia sevata sevata** (Feld.).

*Field Name*: Faint-scalloped White.

*Species Range*: Central America to Bolivia.

*Subspecies Range*: Colombia and Venezuela.

*Field Characters*: Scalloped border faint and confined to forewing.

*Number*: Rare, only a single specimen taken. Flying in a dense flock of other pierids.

*Record*: 1948—June 6 (male).

**Itaballia demophile demophile** (Linn.).

*Field Name*: Black-bordered Notched White.

*Species Range*: Central America to Paraguay.

*Subspecies Range*: Colombia and Venezuela.

*Field Characters*: A medium white with notched black border.

*Number*: Rare. Taken, 6.

*Record*: 1946—May 28 (2). 1948—July 14 (1), 15 (1), 16 (1), 21 (1, No. 481278).

**Itaballia pandosia pandosia** (Hew.).

*Field Name*: Small Monkeyfaced White.

*Species Range*: Central America to Peru and Trinidad.

*Subspecies Range*: Venezuela and Trinidad.

*Field Characters*: Smaller, otherwise similar to *demophile*.

*Number*: Rare. A single specimen taken in company with 11 other species of pierids.

*Record*: 1948—July 8 (female).

**Pieris mandela mandela** Feld.

*Field Name*: Yellow and Red Underwing.

*Species Range*: Central America to Venezuela and Bolivia.

*Subspecies Range*: Venezuela.

*Field Characters*: Black-bordered white, enclosing white spot in the forewing tip. Dark-veined below, with yellow and red spots.

*Number*: Rare. Taken, 5.

*Date*: June 10 to July 15.

*Record*: 1948—June 10 (1); July 14 (3 females), 15 (1).

**Anteos clorinde clorinde** (God.).

*Field Name*: Giant Orange-spot.

*Species Range*: Texas to Mexico and Paraguay.

*Subspecies Range*: Colombia and Venezuela to Paraguay.

*Field Characters*: Wing spread three and one-quarter inches. Greenish-white with large yellow spot on forewings.

*Number*: Identified several times on the wing, but taken only once.

*Record*: 1948—July 5 (No. 481090).

**Anteos maerula** (Fab.).

*Field Name*: Male: Giant Yellow-green Catopsilia; Female: Giant Greenish-white Catopsilia.

*Species Range*: Mexico to Peru, Venezuela and Trinidad.

*Field Characters*: Male, hardly to be told from *Phoebis eubule marcellina* female, not unlike *A. chlorinde*. It is the largest pierid, three and a half inches in extent.

*Number*: Probably not rare, but seldom permitted exact identification in the field. Taken, 7.

*Sex*: Both sexes taken.

*Date*: March 26 to August 8.

*Record*: 1945—June 20 (female), 21 (male and female). 1948—March 26 (female, No. 48337), April 21 (female, No. 48442), June 6 (female), August 8 (male, taken on board *Santa Paula*, flying with others eastward, off Puerto Cabello, thirty miles northwest of Portachuelo Pass.

**Phoebis agarithe agarithe** (Bois.).

*Field Name*: Orange Catopsilia.

*Species Range*: United States to Paraguay.

*Subspecies Range*: Central America to Paraguay.

*Field Characters*: Medium rich orange pierid; female with slight border.

*Number*: Noted a number of times, but only 3 specimens taken.

*Date*: May 25 to July 26.

*Record*: 1946—May 25 (2, male and female). 1948—July 26 (1).

**Phoebis rurina** (Feld.).

*Field Name*: Male: Large, Yellow, Tailed Catopsilia. Female: Large, Red-edged Catopsilia.

*Species Range*: Venezuela, Colombia, Ecuador and Peru.

*Field Characters*: Male is larger, but sometimes as orange as *P. agarithe*; female is unique in the broad red border to the hindwing.

*Number*: Observed many times. Taken, 26.

*Sex*: Both sexes taken.

*Date*: April 15 to July 28.

*Record*: 1946—May 25 (17 males and 4 females taken); June 8 (1000's seen). 1948—April 29 (female taken, 16 seen), 30 (61 seen); May 1 (female, 29 seen), 8 (105 counted); June 6 (male); July 14 (female), 23 (male).

**Phoebis sennae (= eubule) marcellina** (Cram.).

*Field Name*: Common Large Green Catopsilia.

*Species Range*: United States to Argentina.

*Subspecies Range*: Sub-tropical America.

*Field Characters*: Our old friend, *Catopsilia eubule,* is hardly recognizable under its new name. This large, greenish catopsilia is common in most tropical places. The female has a slight border.

*Number*: Vast numbers seen migrating in waves. Taken, 7.

*Sex*: Both sexes taken.

*Date*: May 4 to July 28.

*Record*: 1945—July 7 (1), 20 (2 taken). 1946—May 4 (246 counted), 25 (3 taken), 27 (100's passing), July 3-8 (large numbers), 10 (1000's migrating), 26 (vast numbers). 1948—June 30 (100's passing); July 15 (1, No. 481557). April 15 to end of July, 100's and 1000's migrating day after day.

**Phoebis statira** (Cram.).

*Field Name*: Lemon Yellow and White Catopsilia.

*Species Range*: South Florida to south Brazil.

*Field Characters*: Proximal half of wings lemon yellow, distal half pale greenish.

*Number*: Common, occasionally in large, dense flocks. Taken, 30.

*Sex*: Both sexes taken.

*Date*: May 5 to July 23.

*Record*: 1946—May 5 (1), 25 (2), 28 (4). 1948—June 6 (14 taken, No. 48735), 17 (2), 20 (2); July 8 (4 taken), 10 (400 an hour), 17 (pouring through the Pass all last week), 23 (1).

Genus **Eurema.**

In journal notes I find the typically colored pierids divided into large, medium and small. On the wing, near at hand, it was often possible to distinguish these three classes. Tens of thousands of pierids passing at a distance day after day, or high in air, were indistinguishable and had to be lumped. Measurements confirmed these divisions; large pierids spreading from 2¾ to 3 inches; medium ones from 2 to 2½ inches; and small from 1¼ to 1¾ inches.

The genus *Eurema* consists altogether of small-sized species. Ten species were migrants and they readily fitted into a pattern and color classification as follows:

Black-tipped Whites.
*albula*
*palmyra* (female)
*phiale*
*xanthochlora* (female)

Black-tipped Yellows.
*dina*
*salome*
*xanthochlora* (male)

Forewing Yellows.
*elathea*
*gratiosa*
*palmyra* (male)
*venusta*

Black-tipped Orange.
*proterpia*

A frequency classification works out as follows:

Abundant.
*alba*
*dire*
*salome*
*venusta*

Common.
*elethea*
*gratiosa*
*palmyra*
*xanthochlora*

Rare.
*phiale*
*proterpia*

**Eurema albula** (Cram.).

*Field Name*: Small Black-bordered White.

*Species Range*: Central America and West Indies to Brazil.

*Field Characters*: A small white pierid, with broad black tips and narrow border. This variable on hindwings but usually present (form *sinoe*). In seven individuals it is absent (form *albula*). Hardly to be told from the female of *palmyra lydia,* except that the hindwing border is scalloped. The latter species is very rare, only 4 specimens having been taken. In the female *elethea* the forewings are washed with yellow.

*Number*: Great numbers seen. Taken, 50. Many others liberated after identification.

*Sex*: Both sexes taken.

*Date*: March 5 to August 8.

*Frequency*: One of the most abundant species. Very few days in 1946 and 1948 passed without seeing or taking them. Sometimes passed singly and steadily, but often in dense flocks or a stream throughout the hours of daylight. The insects often alighted, sometimes from weariness, again to avoid the impact of high winds. Swallows, dragonflies and robberflies all took toll.

*Record*: These are a few from many notes. 1946—May 23 (3, No. 46488, 100's of a fresh brood, fighting against a hard head wind), 28 (3 taken, 100's upon 100's seen), 29 (24 taken, 1000's passing), 31 (more migrating than before); July 3 (1000's low and high, in high wind), 5 (650 in twenty minutes), 18 (2, No. 46786, 100's passing); August 8 (hosts passing for hours). 1948—March 5 (100's); May 23 (2 taken among 100's, among 13 other species of pierids), 26 (50 in two minutes); June 5 (heavy migration), 6 (passing all day), 9 (10's of 1000's in dense flocks), 11 (still great numbers), 18 and 19 (passing for hours, too fast to count), 23 (4, No. 48825), 30 (still abundant). Abundant from July 1 to 29.

**Eurema dina leuce** Bois.

*Field Name*: Small Forewing-bordered Yellow.

*Species Range*: Southern United States and West Indies to Argentina.

*Subspecies Range*: Panama and South America.

*Field Characters*: On the wing, this is indistinguishable from *salome* or from *xanthochlora* males except under most favorable conditions. As *dina* and *salome* are abundant, and *xanthochlora* is common, this confusion covers tens of thousands of individuals. The generous number taken of each species, or taken and liberated after examination, forms the basis for specific identification.

*Number*: Judging by those taken or identified, the total migrants must have been of the order of tens of thousands of the present species. Taken or examined, 58.

*Sex*: Both sexes taken.

*Date*: May 5 to July 28.

*Record*: 1948—May 5, 28; June 6, 7, 28; July 2, 8, 12, 15, 16, 21, 28, etc., etc.

**Eurema elathea** (Cramer), form **medutina** (Feld.).

*Field Name*: Small Bar-wing.

*Species Range*: Southern United States to Argentina.

*Field Characters*: Male with its transverse forewing bar can be confused only with the male *palmyra*. The female with its yellow forewing resembles *gratiosa* and *venusta*.

*Number*: A very common species. Many thousands seen and two dozen taken.

*Sex*: Both sexes taken.

*Date*: May 9 to August 7.

*Frequency*: Flocks of many thousands. Many taken.

*Record*: A few taken in 1945. 1946—May 11, 29 (19 taken); June 7; July 5; August 7 (1,500 in an hour). 1948—May 9, 23, 24, 25, 29; June 6, 17, 30; July 5, 9, 15, 16, 24, 26, etc., etc.

**Eurema gratiosa** (Doubl. & Hew.).

*Field Name*: Small Orange-spot.

*Species Range*: Honduras to Colombia, Venezuela, Trinidad and north Brazil.

*Field Characters*: The usually wide black border, with yellow fore and white hindwings, and especially large orange spot on fore-edge of hindwing distinguish this species. The first character can be made out on the wing.

*Number*: Large numbers must have passed unidentified. Taken, 31.

*Sex*: Both sexes taken.

*Date*: May 23 to August 2.

*Record*: 1945—July 16 (1), 20 (1). 1946—May 29 (8 taken, 100's seen); July 17 (10 taken, 100's passing with others, 18 caught and examined). 1948—May 23 (2), 25 (1), 29 (1), 30 (1); July 5 (1), 8 (1), 21 (1), 23 (1); August 4 (4 taken).

**Eurema palmyra lydia** (Feld.).

*Field Name*: Black-bar (male).

*Species Range*: Central America and West Indies to Brazil.

*Subspecies Range*: Costa Rica to Venezuela.

*Field Characters*: The black-barred male is indistinguishable from the male *elathea*, but the female lacks all yellow.

*Number*: Doubtless many not identified, but two certain flocks, and many single ones examined. Taken, 16.

*Sex*: Both sexes taken.

*Date*: May 23 to July 21.

*Record*: 1946—May 28 (2 taken), 29 (5 taken. 1948—May 23 (1); June 6 (2); July 8 (2), 15 (1), 16 (1), 21 (1), 26 (1).

**Eurema phiale columbia** (Feld.).

*Field Name*: Small Yellow-edged White.

*Species Range*: Colombia, Bolivia to Guianas and Brazil.

*Subspecies Range*: Colombia, Venezuela and Bolivia.

*Field Characters*: A small white pierid, with wide forewing border, and a yellow stain around the hindwing edge.

*Number*: A single specimen taken.

*Record*: 1948—July 13 (1 taken).

**Eurema proterpia proterpia** (Linn.).

*Field Name*: Small Black-bordered Orange.

*Species Range*: Texas to Ecuador.

*Subspecies Range*: Texas to Venezuela.

*Field Characters*: This would be an easy species to identify on the wing on account of its general rich orange color. Unfortunately it seems to be very rare.

*Number*: A single specimen taken.

*Record*: 1946—July 3 (1 taken, No. 46725).

**Eurema salome** (Feld.), form **salome.**

*Field Name*: Small Black-bordered Yellow.

*Species Range*: Mexico to Bolivia and Venezuela.

*Field Characters*: The male is easily confused with *dina* and the male *xanthochlora.* The female is characterized by a distinct pointed tail on the hindwing.

*Number*: Several notes on the female in life, together with many taken show this as one of the four abundant species. Taken, 30.

*Sex*: Both sexes taken.

*Date*: March 16 to October 7.

*Frequency*: Seldom singly. Often with other small pierids.

*Record*: 1945—March 16 (1); April 12 (5); October 7 (1). 1946—April 27 (8 taken, heavy migration, 1,840 counted). 1948—April 17 (1, No. 48372), 27 (1, No. 48411), 30 (1); May 9 (2), 15 (1), 21 (1), 23 (2), 26 (1), 29 (4 taken); June 6 (2), 11 (1), 14 (1), 22 (1), 30 (1); July 3 (1, No. 481029), 4 (2), etc., etc.

**Eurema venusta** Bois., forms **venusta** and **limbia** (Feld.).

*Field Name*: Small Yellow-forewing.

*Species Range*: Colombia, Venezuela, Guianas and Amazonia.

*Field Characters*: The yellow forewing with its wide black border is a good character except in the case of the female *elathea.*

*Number*: Swarms of this species came through the Pass week after week, and seldom a day without seeing them. One of the most abundant insect migrants.

*Sex*: Both sexes taken.

*Date*: April 30 to July 28.

*Record*: For the year 1948 the following represent captures of one to ten on each date: 1948—April 30; May 14, 23, 24, 25, 26, 29; June 6, 7, 22, 24, 28; July 3, 5, 8, 13, 14, 15 (15 taken), 16, 21 (13 taken), 23, 24, 28, etc., etc. Swarms of many thousands passed on May 26, June 6, July 5, 8 and 21.

**Eurema xanthochlora xanthochlora** (Koll.), female form **marjoris** Klots.

*Field Name*: Forewing-bordered Yellow (male); Forewing-bordered White (female).

*Species Range*: Central America, Colombia, Peru and Bolivia.

*Subspecies Range*: Colombia, Venezuela and Brazil.

*Field Characters*: Male with its yellow color and the black-bordered forewing is close to *dina* and *salome.* The whitish female with broad border confined to the forewing is easy to tell under favorable conditions.

*Number*: Taken, 11. Many examined and liberated.

*Sex*: Both sexes taken.

*Date*: April 30 to July 26.

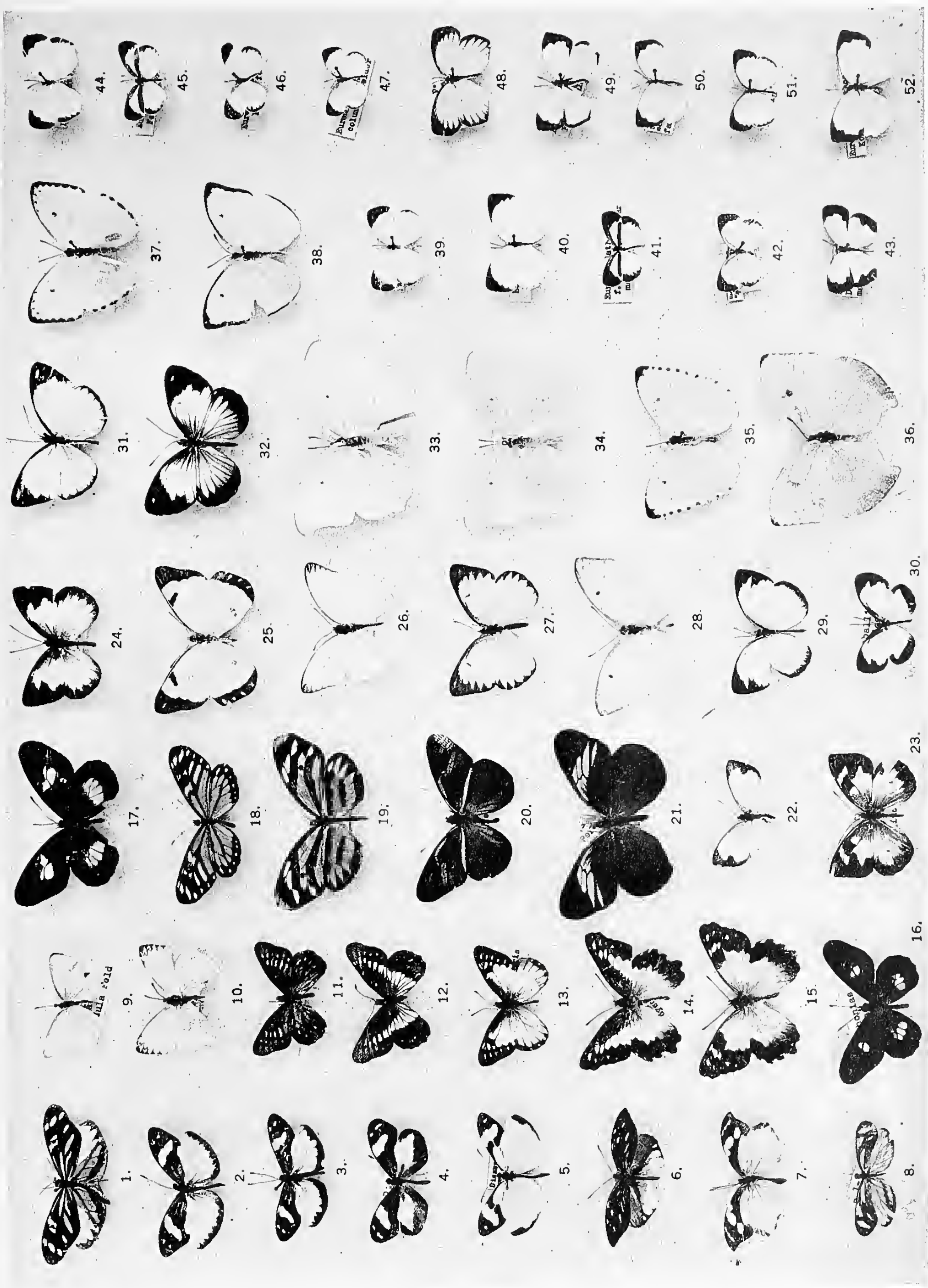
*Record*: 1948—April 30 (1); May 9, 23, 25, 28; July 3, 8, 14, 15, 23, 26. These dates represent the major number of captures or examinations.

## EXPLANATION OF THE PLATE.

### Plate I.

Forty-four species of butterflies of the family Pieridae taken as migrants at Portachuelo Pass, Rancho Grande, north-central Venezuela.

Fig. 1. *Dismorphia amphione astynomides* (male).
Fig. 2. *Dismorphia critomedia.*
Fig. 3. *Dismorphia hyposticta.*
Fig. 4. *Dismorphia medora medora.*
Fig. 5. *Dismorphia melite.*
Fig. 6. *Dismorphia nemesis nemesis* (male).
Fig. 7. *Dismorphia nemesis nemesis* (female).
Fig. 8. *Dismorphia theucharila theucharila.*
Fig. 9. *Pseudopieris nehemia virdula.*
Fig. 10. *Hesperocharis marchalii marchalii.*
Fig. 11. *Catasticta crowleyi.*
Fig. 12. *Catasticta flisa flisa.*
Fig. 13. *Catasticta prioneris albescens.*
Fig. 14. *Leodonta dysoni dysoni.*
Fig. 15. *Leodonta tagaste marginata.*
Fig. 16. *Archonias tereas critias* (male).
Fig. 17. *Archonias tereas critias* (female).
Fig. 18. *Charonias eurytele caraca.*
Fig. 19. *Pyrrhybris pyrrha malenka.*
Fig 20. *Pereunte charops meridana* (male).
Fig. 21. *Pereunte charops meridana* (female).
Fig. 22. *Leptophobia aripe aripe.*
Fig. 23. *Leptophobia penthica stamnata.*
Fig. 24. *Leptophobia tovaria tovaria.*
Fig. 25. *Melete lycimnia eurymnia.*
Fig. 26. *Andropodum drusilla drusilla.*
Fig. 27. *Ascia monuste monuste.*
Fig. 28. *Ascia sevata sevata.*
Fig. 29. *Itaballia demophile demophile.*
Fig. 30. *Itaballia pandosia pandosia.*
Fig. 31. *Pieris mandela mandela* (male).
Fig. 32. *Pieris mandela mandela* (female).
Fig. 33. *Anteos chlorinde chlorinde.*
Fig. 34. *Anteos maerula.*
Fig. 35. *Phoebis agarithe agarithe.*
Fig. 36. *Phoebis rurina.*
Fig. 37. *Phoebis sennae marcellina.*
Fig. 38. *Phoebis statira.*
Fig. 39. *Eurema albula.*
Fig. 40. *Eurema dina leuce.*
Fig. 41. *Eurema elathea.*
Fig. 42. *Eurema gratiosa* (male).
Fig. 43. *Eurema gratiosa* (female).
Fig. 44. *Eurema palmyra lydia* (male).
Fig. 45. *Eurema palmyra lydia* (female).
Fig. 46. *Eurema phiale columbia.*
Fig. 47. *Eurema proterpia proterpia.*
Fig 48. *Eurema salome* (male).
Fig. 49. *Eurema salome* (female).
Fig. 50. *Eurema venuste.*
Fig. 51. *Eurema xanthochlora xanthochlora.*



MIGRATION OF PIERIDAE (BUTTERFLIES) THROUGH PORTACHUELO PASS,
RANCHO GRANDE, NORTH-CENTRAL VENEZUELA.

# 17.

# Moths New to Trinidad, B.W.I.[1]

NORMAN LAMONT & E. MCC. CALLAN.

Edited by William Beebe.

## INTRODUCTION.

Twenty-four years have passed since the publication of "A Catalogue of the Trinidad Lepidoptera Heterocera (Moths)" by William James Kaye, F.E.S., and Sir Norman Lamont, Bt. This appeared in 1927 as Number Three of the Memoirs of the Department of Agriculture, Trinidad and Tobago, Port-of-Spain, Trinidad. It contained the names and brief data concerning 1,016 species and subspecies of Trinidad moths.

In 1941 Sir Norman prepared a further list of 150 species, bringing the Trinidad moths up to date. This remained unpublished, and finally, just before his death, Sir Norman expressed his hearty willingness to have me edit and publish the additional list.

It seems appropriate to print the following paragraphs from the introduction written by the late Sir Norman for his list:

"The number of moths in the first catalogue was 1016, and now 150 are added, principally from my own captures and from records given in Seitz's monumental volumes. The combined total of 1166 species can, however, bear little real relation to the total number inhabiting Trinidad.

"It will be observed that several of the more interesting captures now recorded came from the Arima Valley and I think that there is little doubt that, if lights were systematically worked in the valleys of the Northern Range, an immense number of interesting captures would be made, of insects new to this imperfect list, and perhaps of some new to science.

"I wish to record my great obligation to three friends for much assistance, both in referencing names and in the determinations of difficult and obscure species, namely, to Mr. W. H. Tams, of the Natural History Museum, South Kensington; to Mr. L. B. Prout of the Zoological Museum, Tring; and to my old collaborator, Mr. W. J. Kaye."

Knockdow. NORMAN LAMONT.
1 Dec., 1941.

At about the same time that Sir Norman gave permission to publish his list, Dr. E. McC. Callan of the Imperial College of Tropical Agriculture gave me a list of 29 additional records of which he has kindly allowed me to make use. I have combined the two lists and now present a total of 179 moths new to the published fauna of the island. This provides an excellent foundation for any future, more comprehensive and intensive research upon the ecology of this group of insects.

WILLIAM BEEBE

[1] Contribution Number 882, Department of Tropical Research, New York Zoological Society.

## FAMILY SYNTOMIDAE.

**Eriphiodes tractipennis** Butler.

Butler, *J. Linn. Soc. Lond. Zool.* 12, p. 414; Draudt, in Seitz, 6, p. 132, pl. 26m.

Range: Common from Honduras to Brazil.

Mayaro, 6 Jan., 1921 (N. L.).

**Mesothen desperata** Walker.

Walker, List Lep. Ins. Brit. Mus. 7, p. 1602; Draudt, in Seitz, 6, p. 66, pl. 12k.

Range: From Panama through Guiana and Brazil as far as Paraguay and Argentina. "Flies in day time; on Compositae."

Palmiste, 20 April, 1926 (N. L.).

**Macrocnene albitarsia** Hampson.

Hampson, Cat. Lep. Phal. 1, p. 325; Draudt, in Seitz, 6, p. 105, pl. 17e.

Range: Amazon.

Palmiste, 26 Feb., 1926; 2 Feb., 1936 (N. L.).

**Eucereon dorsipunctum** Hampson.

Hampson, *Ann. Mag. Nat. Hist.*, (7) 15, p. 430; Draudt, in Seitz, 6, p. 174.

Range: Venezuela, Brazil, Paraguay.

Palmiste, 14 Feb., 1934 (N. L.).

**Amycles affinis** Rothschild.

Rothschild, *Novit. Zool.*, XIX, p. 153.

Range: Mexico to Venezuela.

Recorded by Vesey-FitzGerald (*Proc. Entom. Soc. Lond.*, (A) 14, 1939, p. 105) as bearing a striking resemblance to the social wasp, *Parachartergus apicalis* (F.).

## FAMILY ARCTIIDAE.

### Sub-family Arctiinae.

**Automolis bonora** Schaus.

Schaus, *Proc. U. S. Nat. Mus.*, 29, p. 219; Seitz, 6, p. 367, pl. 50g.

Range: French Guiana.

Palmiste, 27 Feb., 1930 (N. L.).

### Sub-family Lithosiinae.

**Agylla fasciculata** Walker.

Walker, List Lep. Ins. Brit. Mus., 2, p. 552; Draudt, in Seitz, 6, p. 282, pl. 36b.

Range: Venezuela, Colombia.

Maupertuis, 9 Feb., 1934 (N. L.).

**Agylla nivea** Walker.

Walker, List Lep. Het. Brit. Mus., 7, p. 1778; Draudt, in Seitz, 6, p. 281, pl. 37c.

Range: Mexico, Panama, Colombia, Ecuador.

Verdant Vale, 10 April, 1919 (N. L.).

## Family Notodontidae.

**Pentobesa xylinoides** Walker.

Walker, Cat. Lep. Het. Brit. Mus., 35, 1886, p. 193; Draudt, in Seitz, 6, p. 913, pl. 144b.
Range: Central America, Colombia.
Palmiste, 7 March, 1934 (N. L.).

**Lysana plusiana** Schaus.

Schaus, *Trans. Ent. Soc. Lond.*, 1901, p. 274; Draudt, in Seitz, 7, p. 920, pl. 144h.
Range: Venezuela, Paraguay.
Palmiste, 26 Dec., 1921 (N. L.).

**Strophocerus thermesia** Felder.

Felder, Reise Novara, 1:97, 1874, f. 9; Draudt, in Seitz, 7, p. 926.
Range: Trinidad, French Guiana, Brazil.
St. Augustine, 10 Nov., 1906 (E. M. Fountain); St. Patricks, Arima, 1 April, 1938 (N. L.).

**Tachuda discreta** Schaus.

Schaus, *Proc. U. S. Nat. Mus.*, 29, 1905, p. 241; Draudt, in Seitz, 7, p. 928, pl. 145g.
Range: Guiana, Brazil, Trinidad, West Indies.

**Marthula luteopunctata** Dognin.

Dognin, *Ann. Soc. Ent. Belge*, 48, p. 115 (1904). Draudt, in Seitz, 6, p. 992, pl. 144.
Range: Peru and Bolivia.
Palmiste, 1 March, 1948.

**Dasylophia guarana** Schaus.

Schaus, *Proc. Zool. Soc. Lond.*, 1882, p. 331; Draudt, in Seitz, 7, p. 932, pl. 146b.
Range: Mexico, Venezuela, Brazil, Peru.
Palmiste, 1 Jan., 1928, and on 30 Jan., 1928, bred out a series of nine, from larvae taken on *Roble* (*Platymiscium*) (N. L.). Reported by Guffy (Board Agri. Trin. Cirl., 3, 1911, f. 12) as a pest of *Roble* and *Poui*.

**Malocampa punctata** Stoll.

Stoll in Cramer, Cramer, Pap. Exot., IV, t. 307, F. (1782); Draudt, in Seitz, 6, p. 981, pl. 151b.
Range: Mexico, Bolivia.
Palmiste, 20 Sept., 1947 (N. L.).

**Malocampa albolineata** Druce.

Druce, Biol. Cent. Amer., Het., I, p. 245 (1887) Draudt, in Seitz, 6, p. 983, pl. 151d.
Range: Mexico to Brazil.
Palmiste, 24 March and 26 April, 1947. (N. L).

**Farigia xenopithia** Druce.

Druce, *Ann. Mag. Nat. Hist.*, (8) 8, 1911, p. 142; Draudt, in Seitz, 7, p. 937.
Range: Trinidad.

**Hippia pronax** Dognin.

Dognin, *Ann. Soc. Ent. Belg.*, 52, 1908, p. 165; Draudt, in Seitz, 6, p. 940, pl. 147b.
Range: "French Guiana, Trinidad, Eastern Peru."

**Lirimiris lignitecta** Walker.

Walker, Cat. Lep. Het. Brit. Mus., 32, 1865, p. 469; Draudt, in Seitz, 7, p. 943, pl. 147d.
Palmiste, 15 Jan., 1936 (N. L.).

**Salluca pistacina** Schaus.

Schaus, *Trans. Ent. Soc. Lond.*, 1901, p. 295. *Phastia maricolor* Kaye, *Proc. Zool. Soc. Lond.*, 1922, p. 992, pl. I, f. 12 (according to Draudt, in Seitz, 7, p. 952).
Range: Costa Rica.
Palmiste, 20 Nov., 1935 (N. L.).

**Talmeca perplexa** Schaus.

Schaus, *Proc. U. S. Nat. Mus.*, 29, 1905, p. 262; Draudt, in Seitz, 7, p. 988.
Range: French Guiana, Trinidad.

**Chadisra peirreta** Dognin.

Dognin, Het. Nouv. Am. Sud., 7, 1914, p. 25; Draudt, in Seitz, 7, p. 992.
Range: Trinidad.

**Talmenia arsilonchoides** Möschler.

Möschler, *Verh.*, 2-6 Grs. 32, 1883, p. 346; Draudt, in Seitz, 7, p. 994.
Range: Brazil, Peru.
Palmiste, 9 Dec., 1931 (N. L.).

**Hemiceras alba** Walker.

Walker, Cat. Lep. Het. Brit. Mus., 33, p. 851; Draudt, in Seitz, 7, p. 1043, pl. 156h.
Range: Mexico.
Palmiste, 9 Dec., 1947.

**Rifargia occulata** Schaus.

Schaus, *Proc. U. S. Nat. Mus.*, 29, 1905, p. 272; Draudt, in Seitz, 7, p. 1001.
Range: French Guiana, Surinam.
St. Patricks, Arima, 21 April, 1938 (N. L.).

**Antaea juturna** Cramer.

Cramer, Pap. Exot., II, t. 129 E; Draudt, in Seitz, 6, p. 1049, pl. 158c.
Range: Panama to Brazil.
Verdant Vale, 29 Nov., 1947 (N. L.).

## Family Noctuidae.

### Sub-family Noctuinae.

**Eulepidotis ezra** (Druce).

*Palindis ezra* Druce, Biol. Cent. Amer., Het. 2, 1898, p. 499, pl. 96, f. 1.
Range: Mexico.
Palmiste, 5 March, 1930 (N. L.).

**Deinopa erecta** (Walker).

*Asthana erecta* Walker, *Trans. Ent. Soc. Lond.*, (3) 1, 1864, p. 101.
Range: British Guiana, Brazil.
St. Patricks, Arima, 20 April, 1930 (N. L.).

**Pseudophisma diatonica** (Möschler).

*Ophiusa diatonica* Möschler, *Verhandl. der K. K. zool.-bot. Gesellschaft Wien*, p. 433, pl. 9, fig. 28 (1880).
Range: British Guiana and Surinam.
Verdant Vale, 5 Feb., 1938 (N. L.).

**Panula inconstans** Guenée.

Guenée, Hist. Nat. Ins. Lepid., VII (Noct. III), 59 (1852).
Range: Jamaica, St. Lucia, Trinidad.
Palmiste, 14 Oct., 1947 (N. L.).

**Eucalyptra** n.sp.

Palmiste, 26 April, 1930 (N. L.).

**Herminiodes modesta** (Warren).

*Chadaca modesta* Warren, *Trans. Ent. Soc. Lond.*, 1889, p. 233.
Range: Panama, British Guiana, Amazons.
Palmiste, 7 Jan., 28 Feb., 2 March, 1932 (N. L.).

**Metalectra ecchlora** Hampson.

Hampson, Descr. Gen. Spec. Noctuinae, 1926, p. 281.
Range: Colombia.
"Trinidad," 1934 (Withycombe), Palmiste, 6 Dec., 1929 (N. L.).

**Renodes aequalis** (Walker).

*Platydia aequalis* Walker, List Lep. Ins. B. M., 34, 1865, p. 1121.
Range: St. Vincent, Colombia, Ecuador, Paraguay.
St. Patricks, Arima, 4 Jan., 1930 (N. L.).

**Athysania sinaldus** (Guenée).

*Gonodonta sinaldus* Guenée, Hist. Nat. Ins. Spec. Gen. Lepid., 6, 1852, p. 372.
Range: Mexico to south-east Brazil.
Palmiste, 21 Jan., 27 April, 1930 (N. L.).

**Betusa chera** (Drury).

*Phalaena noctua chera* Drury, Ill. Nat. Hist. (Exotic Insects), II, p. 36, pl. 20, fig. 4, Index p. 1, (1773).
Range: Surinam.
St. Joseph, March, 1922. Palmiste, 14 Oct., 1947 (N. L.).

**Antiblemma discomaculata** (Brabant).

*Caprodes discomaculata* Brabant, *Le Naturaliste*, 32, 1911, p. 187.
Palmiste, 27 March, 1934 (N. L.).

**Antiblemma addana** (Schaus).

*Caprodes addana* Schaus, *Ann. Mag. Nat. Hist.*, (8), 8, 1911, p. 226.
Range: Chiriqui.
Palmiste, 15 Nov., 1933 (N. L.).

**Tyrissa perstrigata** Schaus.

Schaus, *Ann. Mag. Nat. Hist.*, (8) 8, 1911, p. 218.
Range: Costa Rica, Brazil.
Palmiste, 10 Nov., 1933 (N. L.).

**Epidroma suffusa** (Walker).

*Thermesia suffusa* Walker, List Lep. Ins. B. M., 15, 1858, p. 1561.
Range: Cuba, Bahamas, West Indies, Brazil, Haiti (type).
St. Patricks, Arima, 27 Nov., 1933, 10 April, 1934 (N. L.).

**Paracoeria**, near **orobaena** Druce.

Palmiste, 21 Dec., 1929 (N. L.).

**Heteropygas**, near **nymbides** Hampson.

Hampson, Descr. Gen. Spec. Noctuinae, 1926, p. 300.
Specimens with Tams for verification as new species.

**Cryptochrostis hyphinoe** (Stoll).

*Phalaena noctua hyphinoe* Stoll, in Cramer, Pap. Exot., IV, pp. 130 and 248, pl. 357, figs. G and H (1781).
Range: Surinam.
Verdant Vale, 1 April, 1938 (N. L.).

**Pseudophisma pritanis** (Cramer).

*Sphinx pritanis* Cramer, *Uitl. Kapell.* 2, 1777, p. 31, 115, f. d.
Range: Brazil, Peru, Paraguay.
St. Patricks, Arima, 26 Jan., 1928 (N. L.).

**Lutogonia simplex** Schaus.

Schaus, *Ann. Mag. Nat. Hist.*, (8) 11, 1913, p. 30.
Palmiste, 21 Dec., 1929 (N. L.).

**Calpe excitans** (Walker).

*Oraesia excitans* Walker, List Lep. Ins. B. M., 12, 1857, p. 942.
Range: Mexico, Santo Domingo, Jamaica.
Palmiste, 4 May, 1934 (N. L.).

**Elousa hadenoides** (Guenée).

*Coxina hadenoides* Guenée. Hist. Nat. Ins. Spec. Gen. Lep., 6, 1852, p. 299.
Range: Mexico, Venezuela.
Palmiste, 13 and 23 Nov., 1933 (N. L.).

Sub-family Acromyctinae (Zenobianae).

**Cropia minthe** (Druce).

*Dyops minthe* Druce, Biol. Cent. Amer., Het. 1, 1889, p. 322, pl. 29, f. 28; Draudt, in Seitz, 7, p. 221, pl. 32c. *Decelea infusa* Kaye & Lamont (*Mem. Dept. Agri. Trinidad and Tobago*, 3, 1927, p. 56), nec Walker.
Range: Panama, Venezuela, Peru.
In Nat. Coll. (F. W. Jackson); Palmiste, 18 Nov., 1927 (N. L.).

**Argyrosticta vau-aurea** (Hampson).

*Argyrostrotis vau-aurea* Hampson, Cat. Lep. Phal., 7, 1908, p. 522; Draudt, in Seitz, 7, p. 238, pl. 35b.
Range: Trinidad, British Guiana.

**Perigea albolabes** Grote.

Grote, *Can. Ent.*, 12, 1880, p. 216; Draudt, in Seitz, 7, p. 226, pl. 33b.
Range: Arizona to Colombia.
Palmiste, 12 March, 1930 (N. L.).

**Perigea poliopastea** Hampson.

Hampson, Cat. Lep. Phal. 7, 1908, p. 308. Draudt, in Seitz, 7, p. 225, pl. 32i.
Range: Guiana, Bolivia, Trinidad.

**Chytonidia commixta** Schaus.

Schaus, *Proc. U. S. Nat. Mus.*, 46, 1914, p. 487; Draudt, in Seitz, 7, p. 244, pl. 35h.
Range: French Guiana.
Palmiste, 9 Feb., 1928 (N. L.).

**Chytonix griseorufa** Hampson.

Hampson, Cat. Lep. Phal., 7, 1908, p. 606; Draudt, in Seitz, 7, p. 244, pl. 35h.
Range: Brazil, Trinidad.

**Catabena esula** (Druce).

*Xylina esula* Druce, Biol. Cent. Amer., Het. 1, 1889, p. 297, pl. 28, f. 1; Draudt, in Seitz, 7, p. 255, pl. 37c.
Range: Texas to Panama, Granada.
Palmiste, 5 Jan., 1938 (N. L.).

**Gonodes liquida** (Möschler).

*Ipimorpha liquida* Möschler, *Abh. Senck. Ges.*, 14, 1886, p. 48, f. 17; Draudt, in Seitz, 7, p. 264, pl. 38d.
Range: Central America, Cuba, Brazil, Paraguay.
Palmiste, 15 Dec., 1933 (N. L.).

**Monodes grata** (Hübner).

*Elaphria grata* Hübner, Zutr. Exot. Schmett., 1, 1818, p. 16, f. 71, 72; Draudt, in Seitz, 7, p. 273, pl. 39c.
Range: Florida, Texas, Mexico, Panama.
Palmiste, 22 Feb., 1938 (N. L.).

**Monodes babarossa** Hampson.

Hampson, Cat. Lep. Phal. 8, 1909, p. 461; Draudt, in Seitz, 7, p. 266, pl. 38e.
Range: Trinidad, Paraguay.

**Monodes agrotina** (Guenée).

*Celaena agrotina* Guenée, Hist. Nat. Ins. Spec. Gen. Lep., 5, 1852, p. 221; = *trientiplaga* Walker = *gattula* H. Sch. = *aduncula* Feld.; Draudt, in Seitz, 7, p. 268, pl. 38f.
Range: Cuba, Venezuela, Guiana, Brazil, Colombia, Jamaica, Paraguay.
Palmiste, 20 Nov., 1929; 30 Dec., 1931; 31 March, 1932 (N. L.).

**Monodes phaeopera** Hampson.

Hampson, Cat. Lep. Phal., 8, 1909, p. 488; Draudt, in Seitz, 7, p. 270, pl. 381.
Range: Venezuela, Colombia.
Palmiste, 22 April, 1928, female; 5 Nov., 1929, male; 15 April, 1930 (N.L.).

**Monodes lithodia** (Schaus).

*Eustrotia lithodia* Schaus, *Trans. Ent. Soc. Amer.*, 30, 1904, p. 154; Draudt, in Seitz, 7, p. 274, pl. 39d.
Range: Brazil, Trinidad.

**Neomilichia caternaulti** (Guenée).

*Perigea caternaulti* Guenée, Hist. Nat. Ins. Spec. Gen. Lep., 5, 1852, p. 233; Draudt, in Seitz, 7, p. 275, pl. 39e.
Range: British Guiana, Venezuela, Amazons.
Palmiste, 7 Feb., 1930 (N.L.), "Trinidad" (Dyar).

**Closteromorpha reniplaga** Felder.

Draudt, in Seitz, 7, p. 302, pl. 44c.
Range: Brazil.
St. Patricks, Arima, 26 Jan., 1928 (N.L.).

**Micrathetis dasarada** (Druce).

*Thalpochares dasarada* Druce, Biol. Cent. Amer., Het. 2, 1898, p. 498, pl. 95, f. 28; Draudt, in Seitz, 7, p. 263, pl. 42a.
Range: Mexico, Costa Rica, Brazil, Cuba, Jamaica.
"Trinidad" (Dyar) in Nat. Coll.

**Bagisara subusta** Hübner.

*Atethmia subusta* Hübner, Samml. Exot. Schmett, II, p. 6, ff. 205-6.
Range: Southern United States to Argentina.
Collected by H. A. Ballou.

Sub-family Hadeninae.

**Cirphis inconspicua** (Herrich-Schaeffer).

*Leucania inconspicua* H.-Sch., *Corresp.-Blatt. Zool. Min. Ver. Regensb.*, 1868, p. 148; Draudt, in Seitz, 7, p. 167, pl. 24i.
Range: Mexico, Cuba, Jamaica.
Palmiste, 14 Dec., 1931 (N.L.).

**Cirphis jaliscana** (Schaus).

*Leucania jaliscana* Schaus, *N. Y. Ent. Soc.*, 6, 1898, p. 114; Draudt, in Seitz, 7, p. 166, pl. 24c.
Range: Mexico.
Palmiste, 25 Nov., 1929 (N.L.).

Sub-family Agrotinae.

**Heliothis armigera** (Hübner).

*Noctus armigera* Hübner, Samml. Eur. Schmett., Noct., 1803-8, f. 370.
Range: World-wide. Corn Earworm. A major pest of corn.
Palmiste, 20 Nov., 1929 (N.L.).

Sub-family Erastriinae.

**Diastema tigris** Guenée.

Guenée, Hist. Nat. Ins. Spec. Gen. Lep., 6, 1852, p. 317, pl. 15, f. 2; Draudt, in Seitz, 7, p. 384, pl. 52k.
Range: Mexico, Panama, Colombia, Venezuela, Granada.
Salybia, 20 Jan., 1928 (N.L.).

Sub-family Euteliinae (Phlogophorinae).

**Eutelia ablatrix** (Guenée).

*Penicillaria ablatrix* Guenée, Hist. Nat. Ins. Spec. Gen. Lep., 6, 1852, p. 303.
Range: Colombia, Jamaica, Haiti, St. Lucia.
Palmiste, 27 April, 1926 (N.L.).

**Eutelia abscondens** (Walker).

*Penicillaria abscondens* Walker, List. Lep. Ins. B. M., 15, 1858, p. 1774.
Range: Costa Rica to Venezuela, Guiana and Brazil.
Golden Grove, 20 July, 1923.

Sub-family Catolinae.

**Ophisma tropicalis** Guenée.

Guenée, Hist. Nat. Ins. Spec. Gen. Lep., 7, 1852, p. 238.

Range: Mexico, Venezuela, Cuba, St. Vincent, Paraguay.

Palmiste, 20 May, 1938 (N.L.).

**Nymbis garnoti** (Guenée).

*Phurys garnoti* Guenée, Hist. Nat. Ins. Spec. Gen. Lep., 7, 1852, p. 306, pl. 23, f. 3.

Range: Grenada, Jamaica, Haiti, St. Lucia.

Palmiste, 15 Nov., 1931 (N.L.).

**Focillidia texana** Hampson.

Hampson, Cat. Lep. Phal., 13, 1913, p. 148.

Range: Texas.

Palmiste, 30 Dec., 1935 (N.L.).

**Metria mascara** (Schaus).

*Campometra mascara* Schaus, *Ann. Mag. Nat. Hist.*, (7), 7, 1901, p. 42.

Range: Venezuela.

Palmiste, 4 April, 1934 (N.L.)

**Calyptis iter** Guenée.

Guenée, Hist. Nat. Ins. Spec. Gen. Lep., 6, 1852, p. 324, pl. 12, f. 3.

Range: Brazil, British Guiana, Paraguay.

Palmiste, 3 Dec., 1933 (N.L.).

Sub-family Phytometrinae (Plusiinae).

**Plusia oxygramma** Geyer.

Geyer, in Hübner, Zutr. Exot. Schmett., 4, 1832, p. 37, f. 769-70.

Range: Mexico, Colombia, Venezuela, Brazil.

Palmiste, 11 Dec., 1933 (N.L.).

Sub-family Hypeninae (Deltoids).

**Megatomis albivia** Hampson, sp.n.

The following description is from the original MS by Hampson. Female: Head, thorax and abdomen dark reddish brown slightly mixed with whitish; antennae blackish, tinged with white toward base; palpi with extremity of second joint white; pectus and legs red-brown mixed with dark brown and ochreous; tarsi ringed black-brown and ochreous; ventral surface of abdomen dark brown irrorated with white. Forewing dark reddish brown, irrorated with ochreous to the post-medial line, especially on costal area, the terminal area dark brown tinged with gray; antemedial line very indistinct, dark brown defined on inner side by ochreous; a minute black point in upper part of middle of cell; yellowish white discoidal striga defined on inner side by dark brown; post medial line blackish defined on outer side by whitish, slightly except below the cell where it is defined by a narrow white band, angled outwards below costa, then inwardly oblique to lower angle of cell where it is slightly bent inwards, then oblique to inner margin; subterminal line indistinct rather diffused blackish with yellowish white striga from costa, then somewhat dentate, oblique below vein 4; a rather wedge-shaped blackish subapical spot; a dark terminal line; cilia yellow at base, with dark brown line at middle, the tips checkered white and dark brown. Hind wing dark reddish brown tinged with gray, slightly irrorated with ochraceous white to the narrow, oblique, almost straight, white postmedial band, which is interrupted at submedian fold; a rather irregularly waved, blackish, subterminal line, slightly defined on inner side by whitish scales; a dark terminal line; cilia yellowish at base, with dark brown line at middle, the tips checkered with whitish and dark brown. Underside dark reddish brown, tinged with gray and irrorated with white except before and beyond the subterminal line; both wings with small, blackish discoidal spot, indistinct dark postmedial line defined on each side by white irroration and waved white subterminal line, on forewing obsolescent between veins 8 and 3, and defined on each side by slight blackish spots above and below vein 7; a black sub-apical spot. Expanse 26 mm. 1 female type.

Range: British Guiana.

Demerara (Rodway); St. Patricks, Arima, 24 Nov., 1929 (N.L.).

**Megatomis submarcata** Schaus.

Schaus, *Proc. U. S. Nat. Mus.*, 50, 1916, p. 340.

Range: French Guiana.

Palmiste, 1913 (N. L.).

**Lascoria phormisalis** Walker.

Walker, List Lep. Ins. B. M., 19, 1859, p. 839.

Range: Brazil, Paraguay, Panama, Guatemala, Costa Rica, Colombia.

Palmiste, 22 Nov., 1933 (N. L.).

**Carteris lineata** (Druce).

*Plynteria lineata* Druce, Biol. Cent. Amer., Het. 1, 1891, p. 489.

Range: Central America.

Palmiste, 9 and 27 Feb., 1932 (N. L.).

**Aglaonice hirtipalpis** (Walker).

*Bleptina hirtipalpis* Walker, List Lep. Ins. B. M., 16, 1858, p. 242.

Range: Mexico, Panama, Venezuela.

Palmiste, 10 March, 1934 (N. L.).

**Oidemastis aeatusalis** (Walker).

*Bleptina aeatusalis* Walker, List Lep. Ins. B. M., 19, 1859, p. 871.

Range: Southern Brazil.

Palmiste, 20 Nov., 1929 (N. L.).

**Argania pilosa** Druce.

Druce, Biol. Cent. Amer., Het. 1, 1891, p. 480.

Range: Guatemala, Brazil.

St. Patricks, Arima, 20 April, 1930 (N. L.).

**Rejectaria** sp.n.

Palmiste, 14 Feb., 1930 (N. L.).

**Ophiuche mactatalis** (Walker).

*Hypena mactatalis* Walker, List Lep. Ins. B. M., XVI, p. 45 (1858).
Range: Costa Rica to Venezuela and Peru.
Caparo, Dec., 1904 (F. Birch).

**Tortricodes orneodalis** Guenée.

Guenée, Hist. Nat. Ins. Spec. Gen. Lep., 8, 1852, p. 73.
Palmiste, 14 Dec., 1927 (N. L.).

FAMILY LYMANTIDAE (LIPARIDAE).

**Phiditia minor** Schaus.

Schaus, *Proc. U. S. Nat. Mus.*, 65, 1924, p. 60; Seitz, 6, p. 556, pl. 75a.
Range: Trinidad, Paraguay.

**Eloria spectra** (Hübner).

*Liparis spectra* Hübner Zutr. Exot. Schmett., 2, 1824; Schaus in Seitz, 6, p. 542, pl. 73e.
Range: Venezuela, Guiana, Trinidad.

FAMILY SPHINGIDAE.

Sub-family Sphinginae.

**Cocytius lucifer** Rothschild.

Rothschild, *Novit. Zool.*, 9, Suppl. 1903, p. 59;=*morgani* Bois.=*rivularis* Butler; Draudt, in Seitz, 7, p. 846, pl. 90b.
Range: Mexico to the Amazons.
Palmiste, 9 Dec., 1937 (N. L.).

Sub-family Sesiinae.

**Isognathus caricae** (Linnaeus).

*Sphinx caricae* Linn., *Mus. Lud. Ulr.*, 1764, p. 350. *I. cacus* Chr.; Draudt, in Seitz, 7, p. 867, pl. 98a.
Range: Venezuela to Rio Janeiro.
Palmiste, Five bred from larvae on Allamanda, emerged 24 April, 1934 (N. L.). Strange that this large and handsome insect should have hitherto escaped observation.

**Grammodia caicus** Cramer.

Cramer, Pap. Exot., 2, 1777, p. 42; Draudt, in Seitz, 7, p. 869, pl. 98d.
Range: Florida to Argentina, Cuba Guiana, Amazons.
Palmiste, 23 Nov., 1929 (N. L.).

FAMILY GEOMETRIDAE.

Sub-family Boarmiinae.

**Semiothisa limbularia** Hübner.

Hübner, Zutr. Exot. Schmett, 1, 1818, p.30, fig. 178 (recte 179) 180.
Range: Surinam.
St. Patricks, Arima, 4 March, 1938 (N. L.).

**Semiothisa confusaria** (Walker).

*Macaria confusaria* Walker, List. Lep. Ins. B. M., 23, 1861, p. 916.
Range: Venezuela.
Palmiste, 1 Jan., 1932 (N. L.).

**Apicia concomitaria** Möschler.

Möschler, *Verh. Zool. Bot. Ges. Wien.*, 31, 1881, p. 398, pl. 17, f. 7.
Range: Venezuela to French Guiana and the Amazons.
Palmiste, 3 March, 1939 (N. L.).

**Apicia vibicaris** Cramer.

Cramer, Pap. Exot., Vol. 1, p. 112, pl. 71d.
Range: Described from Surinam.
Collected by H. A. Ballou.

**Pero stolidata** Guenée.

Guenée, Hist. Nat. Ins. Spec. Gen. Lep., 9, 1858, p. 158.
Range: Guatemala to Venezuela, Peru, Brazil and Argentina.
St. Patricks, Arima, 27 Jan., 1938 (N. L.).

**Boarmia umbellularia** Hübner.

Hübner, Zutr. Exot. Schmett, 3, 1825, p. 12, f. 429-430.
Range: Colombia, Venezuela and Brazil.
St. Patricks, Arima, 22 March, 1928 (N. L.).

**Ischnopteryx brylfera** Felder.

Felder, Reise Novara, Zool. 2 (5), 1875, pl. 131, f. 28.
Range: Venezuela to French Guiana.
Palmiste, 30 March, 1939 (N. L.).

**Bagodares pallidicosta** Warren.

Warren, *Novit. Zool.*, 12, 1905, p. 358.
Range: Cuba, Venezuela, Ecuador, Peru and Brazil.
St. Patricks, Arima, 26 Jan., 1930 (N. L.).

**Nepheloleuca semiplaga** Warren.

Warren, *Novit. Zool.*, 1, 1894, p. 450.
Range: Venezuela, Brazil.
Palmiste, 20 Jan., 1926 (N. L.).

**Stenalcidia congruata** Walker.

Walker, List Lep. Ins. B. M., 26, 1862, p. 1219. *S. farinosa*, Warren, *Novit. Zool.*, 4, 1897, p. 471.
Range: Costa Rica, Venezuela.
St. Patricks, Arima, 24 Jan., 1930 (N. L.).

**Opisthoxia nitidisquama** Warren.

Warren, *Novit. Zool.*, 4, 1897, p. 461.
Range: Guiana, Venezuela.
St. Anns, Port-of-Spain, 11 Aug., 1931 (P. L. Guppy). "Taken at electric light. Alights with wings held upright, semi-closed. Walks rapidly."

**Chloropteryx** sp.

St. Augustine, 1945, from larva feeding on inflorescence of *Cordia macrostachya*, R. G. Donald (det. H. W. Capps).

**Eupithecia** sp.

St. Augustine, 1945, from larva feeding on inflorescences of *Cordia macrostachya*, R. G. Donald (det. H. W. Capps).

Sub-family Larentiinae (Phlogophorinae).

**Amaurinia olivacea** Felder.

Felder, Reise Novara, Zool. 2 (5), 1875, pl. 128, f. 13.

Range: Costa Rica to Bolivia and Brazil.

Palmiste, 13 Nov., 1929; 17 Feb., 1930 (N. L.).

**Eois pseudobada** Dognin.

Dognin, Het. Nouv. Amer. Sud, 14, 1918, p. 11.

Range: Central America, West Indies and Venezuela.

Palmiste, 3 Dec., 1933 (N. L.).

Sub-family Hemitheinae.

**Racheospila superaddita** Prout.

Prout, *Novit. Zool.*, 20, 1913, p. 416; Prout in Seitz, 8, p. 39, pl. 4e.

Range: Mexico to Bolivia, Trinidad and Amazons.

Sub-family Oenochrominae.

**Achlora maronii** Thierry-Mieg.

Thierry-Mieg, *Miscell. Ent.*, 22, 1915, p. 46; Prout, in Seitz, 8, p. 13, pl. 1g.

Range: Maroni River, Gorgona Island, Trinidad.

**Semaeopus oaxacana** Schaus.

Schaus, *Trans. Ent. Soc. Amer.*, 27, 1901, p. 189. *Semaeopus distans* Warren, *Novit. Zool.*, 11, 1904, p. 36. Prout, in Seitz, 8, p. 84.

Range: Colombia, Venezuela, Mexico, Trinidad.

**Semaeopus caparonensis** Prout.

Prout, in Seitz, 8, 1936, p. 82, pl. 10d.

Range: Caparo, type male (S. M. Klages) and allotype (F. Birch) in the Tring Museum.

**Acratodes vitticostata** Warren.

Warren, *Proc. U. S. Nat. Mus.*, 30, 1906, p. 460; Prout, in Seitz, 8, p. 131.

Range: "Trinidad, the Guianas, the Amazons, and into Peru; type from French Guiana."

**Acratodes adela** Dognin.

Dognin, *Le Naturaliste*, 12, 1890, p. 18; Prout, in Seitz, 8, p. 130, pl. 15d.

Range: "From Costa Rica to Bolivia in the west, and from Trinidad to Rio Janeiro in the east."

**Scelolophia desmogramma** Dyar.

Dyar, *Ins. Ins. Mens.*, 1, 1913, p. 87; Prout, in Seitz, 8, p. 133.

Range: "Trinidad and Venezuela to Para and Pernambuco; type from French Guiana."

**Scelolophia uniformata** Warren.

Warren, *Novit. Zool.*, 7, 1900, p. 151; Prout, in Seitz, 8, p. 133.

"Only known from the male, which is certainly very close to *sub-roseata*."

FAMILY SATURNIIDAE.

**Automeris nausica** Cramer.

Cramer, Pap. Exot., 3, t, 249 D. E., 1779; Draudt, in Seitz, 7, p. 745-6, pl. 3 B. C.

Range: Guiana, Peru, Bolivia and Trinidad.

**Hylesia mystica** Dyar.

Dyar, *Proc. U. S. Nat. Mus.*, 44, 1913, p. 131; Draudt, in Seitz, 7, p. 758.

Range: Guiana, Trinidad.

**Automeris liberia** Cramer.

Cramer, Pap. Exot., 3, t., 268 F., 1780.

Recorded by Urich (*Bull. Dept. Agric. Trinidad and Tobago*, 14, 1915, p. 202) as a pest of cocoanut. Pap. Exot., III, t. 268 F.

Range: Venezuela, Guiana, Colombia, Brazil, Peru.

FAMILY BOMBYCIDAE.

**Anticla antica** Walker.

Walker, List Lep. Ins. B. M., 5, 1855, p. 1174=*eutilla* Druce=*carya* Druce=*amylca* Druce; Schaus, in Seitz, 6, p. 691, pl. 89i.

Range: Costa Rica, Panama, Colombia, Venezuela, Peru.

St. Patricks, Arima, 4 March, 1938 (N. L.).

**Olceclostera maya** Schaus.

Schaus, *Proc. Zool. Soc. Lond.*, (1892), p. 326; Draudt, in Seitz, 6, p. 705, pl. 141g.

Range: Mexico.

Palmiste, 10 March, 1948 (N. L.).

FAMILY CERATOCAMPIDAE.

**Citheronia penelope** Cramer.

Cramer, Pap. Exot., 2, 1775, C. 45, A. *Eacles cybele* Druce = *ducalis* Walker; Draudt, in Seitz, 7, p. 802, pl. 133b.

Range: Trinidad to south Brazil.

St. Patricks, Arima, 3 April, 1938 (N. L.).

**Citheronia hamifera** Rothschild.

Rothschild, *Novit. Zool.*, 14, 1907, p. 422; Draudt, in Seitz, 7, p. 800.

Range: British Guiana, Trinidad.

**Homoeopteryx prona** Jordan.

Jordan, *Novit. Zool.*, 31, 1924, p. 177. *Oxytenis malacena* Druce, Biol. Cent. Amer., Het. 1, 1886, p. 198; Draudt, in Seitz, 7, p. 818, pl. 122b.

Range: Trinidad, British Guiana.

Maupertuis, 22 Jan.; Palmiste, 29 March, 1932 (N. L.).

FAMILY EPIPLEMIDAE.

**Nedusia** sp.n.

One in Nat. Hist. Museum from S. E. Peru.

Palmiste, 29 May, 1938 (N. L.).

**Molybdophora concinnaria** Hübner

Hübner, Zutr. Exot. Schmett., f. 199; Gaede, in Seitz, 7, p. 1168, pl. 172g.

Range: Guatemala, British Guiana, Brazil.

St. Patricks, Arima, 24 Nov., 1929 (N. L.).

FAMILY LASIOCAMPIDAE.

**Hydrias gibea** Druce.

Druce, *Ann. Mag. Nat. Hist.*, (7) 3, 1899, p. 472. = *Euglyphis macasibia* Strd. = *Hydrias gibea;* Draudt, in Seitz, 6, p. 594, pl. 83c.
Range: Venezuela, French Guiana, Peru, Brazil.
St. Patricks, Arima, 29 Nov., 1937 (N. L.).

**Titya proxima** Burmeister.

Burm. Descr. Arg. V. P., 460, (1878). Draudt, in Seitz, 6, p. 584, pl. 80d. *argentina* Schaus.
Range: Mexico to Paraguay.
Palmiste, 25 Dec., 1947 (N. L.).

FAMILY MEGLAOPYGIDAE.

**Trosia dimas** Cramer.

Cramer, Pap. Exot., 1, 1779, p. 91. *T. tricolora* Fab.
Range: Trinidad (Walter Hopp, in Seitz, 6, p. 1081).

**Macara nigripes** Dyar.

Dyar, *Zool. N. Y.*, 1, 1910, p. 137; W. Hopp, in Seitz, 6, p. 1083.

**Aithorape albicostata** Hopp.

Hopp, *Mitt. Zool. Mus. Berl.*, 13, 1927, p. 256; W. Hopp, in Seitz, 6, p. 1075.
Range: Trinidad, Lower Amazons, Minas Geraes, Paraguay.

**Aidos amanda** Stoll.

Stoll, Stoll in Cramer, Pap. Exot., p. 383. (1782); Hopp, in Seitz, 6, p. 1099, pl. 164a.
Range: Mexico to Paraguay.
Palmiste, 6 July and 11 Nov., 1947 (N. L.).

FAMILY LIMACODIDAE.

**Camila clarissa** Stoll.

Stoll, Stoll in Cramer, Pap. Exot., Suppl., 1790, pl. 34, f. 3. *Miresa clarissa* Dyar, in Seitz, 6, p. 1121. pl. 165d.
Range: Mexico, Colombia, Venezuela, Brazil.
St. Patricks, Arima, 27 Jan., 1934 (N. L.).

**Sibine modesta** Cramer.

Cramer, *Uitl. Kapell.*, 2, 1779, p. 28, pl. 115, f.c. *?iolans* Dyar, in Seitz, 6, p. 1109.
Range: Guatemala, Venezuela, Brazil.
In Nat. Hist. Museum from Trinidad (W. J. Kaye).

**Natada nigripuncta** Barnes & McDunnough.

Barnes & McDunnough, *N. Y. Ent. Soc.*, 18, 1910, p. 161. *Perola sardites* Druce, *Ann. Mag. Nat. Hist.*, (7), 5, 1900, p. 512; Dyar, in Seitz, 6, p. 1125.
Range: Guatemala.
Palmiste, 20 March, 1928 (N. L.).

**Sisyrosea elaeasa** (Dyar).

*Euprosterna elaeasa* Dyar, in Seitz, 6, p. 1122, pl. 165f. *E. avellana* Dognin.
Range: Honduras, Colombia, Guiana, Brazil.
In Nat. Coll., Caparo (F. Birch), (F. W. Urich). Larva on cocoanut (Urich).

**Sisyrosea repetita** (Druce).

*Perola repetita* Druce, *Ann. Mag. Nat. Hist.*, (7), 5, 1900, p. 512; Dyar, in Seitz, 6, p. 1127, pl. 166b.
Range: Costa Rica, Colombia, Venezuela, Guiana, Brazil.
St. Patricks, Arima, 5 Jan., 1936 (N. L.).

**Phobetron hipparchia** (Cramer).

*Euryda hipparchia* Cramer, Pap. Exot., 1777, pl. 185d. *Phobetron coras* Stoll = *variolaris* H.-Sch. = *hipparchia;* Dyar, in Seitz, 6, p. 1132, pl. 166h.
Range: Guatemala, Panama, Brazil.
Palmiste, 1932 (N. L.).

**Semyra** sp. n.

Palmiste, 22 Dec., 1927 (N. L.).

FAMILY TERAGRIDAE.

**Langsdorfia lunifera** (Dyar).

Dyar, in Seitz, 6, p. 1282.
St. Augustine, 1945, from larva boring in woody stems of *Cordia macrostachya*, R. G. Donald (det. Carl Heinrich).
Range: Guatemala to Ecuador and Guianas.

FAMILY THRYIDIDAE.

**Draconia stenoptila** Warren.

Warren, *Novit. Zool.*, 15, p. 331; Gaede, in Seitz, 7, p. 1209, pl. 175h.
Range: Honduras, Trinidad.

FAMILY PYRALIDAE.

Sub-family Epipaschiinae (Pococerinae).

**Pococera elegans** Schaus.

Schaus, *Ann. Mag. Nat. Hist.*, (8), 9, 1912, p. 658.
Range: Costa Rica.
Palmiste, 30 Dec., 1931 (N. L.).

**Jocara** sp.n.

St. Patricks, Arima, 26 Jan., 1930 (N. L.).

**Stericta abrupta** Zeller.

Zeller, *Hor. Soc. Ent. Ross.*, 16, p. 189, pl. 11, f. 16.
Range: Panama, Colombia.
Palmiste, 19 Nov., 1931 (N. L.).

**Macalla thrysisalis** Walker.

Walker, List Lep. Ins. B. M., 16, 1858, p. 156.
Range: Bahamas, Honduras.
Trinidad, 1908 (W. J. Kaye); Palmiste, 3 Jan., 1928 (N. L.).

**Macalla ochrotalis** Hampson.

Hampson, *Ann. Mag. Nat. Hist.*, (7), 17, 1906, p. 139.
Range: Colombia, Venezuela.
Palmiste, 30 Dec., 1935 (N. L.).

Sub-family Chrysauginae (Siginae).

**Hyalosticta** sp.n.

St. Patricks, Arima, 20 April, 1930 (N. L.).

Sub-family Phycitinae.

**Elasmopalpus rubedinellus** (Zeller).

Zeller, *Isis von Oken*, p. 885, 1848.
Range: Central America.
St. Augustine, 16 March, 1940, from pods of pigeon pea (*Cajanus indicus*), M. D. French-Mullen (det. Carl Heinrich). Pigeon pea moth borer. A major pest.

**Ephestia figulilella** Gregson.

Gregson, *The Entomologist*, 5, p. 385, 1871.
Range: Cosmopolitan.
Recorded by Knapp (*Bull. Imp. Inst. Lond.*, 19, 1921, p. 191) as a pest of stored cacao beans.

**Mescinia** sp.

St. Augustine, 6 April, 1948, from larva feeding on dahlia flowers, E. McC. Callan (det. Carl Heinrich).

**Fundella pellucens** (Zeller).

Zeller, *Isis von Oken*, 41, p. 866, 1841.
Range: Florida, West Indies, South America.
A pest of beans and cowpeas. Collected by H. A. Ballou.

Sub-family Crambinae.

**Diatraea impersonatella** (Walker).

*Crambus impersonatellus* Walker, List Lep. Ins. B. M., 27, 1863, p. 163.
"In considerable number in some Trinidad cane-fields; and a minor pest of cane in S. America. Not present in Barbados" (R. W. E. Tucker, *Trop. Agri.*, 17, No. 7, p. 133).

**Diatraea minimifacta** Dyar.

Dyar, *Ent. News*, 22, 1911, p. 202.
Range: Venezuela, French Guiana.
Maraval, July, 1891 (Cited by Box, *Bull. Ent. Res.*, 22, 1931, p. 21).

**Diatraea bellifactella** Dyar.

Dyar, *Ent. News*, 22, 1911, p. 205.
Range: Grenada, Bolivia, Peru, Brazil.
Port-of-Spain (F. Birch, cited by Box, *Bull. Ent. Res.*, 22, 1931).

**Diatraea albicrinella** Box.

Box, *Bull. Ent. Res.*, 22, 1931, p. 34, pl. 5, f. 15.
Range: Ecuador, Peru, British Guiana, Brazil.
Nariva Swamp, 13 Oct., 1934 (H. E. Box), Caroni Swamp, and other localities, larvae in *Panicum grande* and *Typha angustifolia* (see Box, *Trop. Agri.*, 12, 1935, p. 221).

Sub-family Galleriinae.

**Myelobia** sp.

St. Joseph, 27 March, 1940, from larva boring in bamboo (*Bambusa vulgaris*), E. McC. Callan (det. Carl Heinrich).

**Galleria mellonella** (Linnaeus).

*Tinea mellonella* Linn., Syst. Nat., 537.
Range: Cosmopolitan.
Wax Moth. St. Augustine, 15 Jan., 1943, from larva boring in comb of honey bee, A. M. Adamson (det. Carl Heinrich).

**Achroia grisella** (Fabricius).

*Phalaena grisella* Fab., Ent. Syst., III, 2, 289.
Range: Cosmopolitan.
Lesser Wax Moth. St. Augustine, 15 Jan., 1943, from larva boring in comb of honey bee, A. M. Adamson (det. Carl Heinrich).

**Corcyra cephalonica** Stainton.

*Melissoblaptes cephalonica* Stainton, *Ent. Mo. Mag.*, 2, p. 172.
Range: Widely distributed.
Rice Moth. Intercepted by Bureau of Entomology and Plant Quarantine, U. S. Dept. Agri.

Sub-family Pyralinae.

**Piletosoma novalis** Walker.

Walker, List Lep. Ins. B. M., 34, 1865, p. 1399.
Range: Guiana, Peru, Brazil.

Sub-family Agroterinae (Pyraustinae).

**Pilocrocis flagellalis** Dognin.

Dognin, *Ann. Soc. Ent. Belge*, 53, 1909, p. 92.
Range: French Guiana.
Palmiste, 23 March (N. L.).

**Pycnarmon striginalis** (Guérin).

*Spilomela striginalis* Guérin, Hist. Nat. Ins. Spec. Gen. Lep., 8, 1854, p. 281.
Range: Panama, Guiana, Peru, Brazil.
Palmiste, 17 Nov., 1935 (N. L.).

**Phostria insolutalis** Möschler.

Möschler, *Abh. Senck. Ges.*, 16, p. 301.
Range: Guatemala, Santo Domingo, Colombia, Venezuela, Guiana, Peru.
Palmiste, 21 Nov. and 19 Dec., 1927 (N. L.).

**Phostria varialis** Walker.

Walker, *Trans. Ent. Soc. Lond.*, (3), 1, p. 122.
Range: British Guiana, Brazil, Ecuador, Peru.
St. Patricks, Arima, 31 Dec., 1927 (N. L.).

**Sylapta proregata** Hampson.

Hampson, *Ann. Mag. Nat. Hist.*, (8), 10, 1912, p. 14.
Range: Brazil, British Guiana.
Palmiste, 27 Nov., 1927 (N. L.).

**Margaronia albicincta** (Hampson).

*Glyphodes albicincta* Hampson, *Proc. Zool. Soc. Lond.*, 1898, p. 737.
Range: Panama, Colombia, Paraguay, Brazil.
Palmiste, 10 March, 1934 (N. L.).

**Margaronia flegia** (Cramer).

*Phalaena flegia* Cramer, *Uitl. Kapell.*, 2, p. 66, pl. 140, f. d.

Range: Mexico to Brazil, Santo Domingo, Jamaica.

Palmiste, 3 Dec., 1933; 11 March, 1934 (N. L.).

**Dichogama redtenbachii** Lederer.

Lederer, *Wien. Ent. Mon.*, 7, p. 396, pl. 13, f. 10.

Range: Cuba, St. Lucia, Bolivia, Brazil, Paraguay.

Palmiste, 15 Nov., 1935 (N. L.).

### Family Pyraustidae.

**Pachyzancla periusalis** (Walker).

*Botys periusalis* Walker, List Lep. Ins. B. M., XVIII, p. 623.

Range: U. S. to Brazil.

Tobacco Leaf-folder. St. Augustine, 8 Dec., 1941, from larva webbing together and feeding on tomato leaves, E. McC. Callan (det. Carl Heinrich).

**Pachyzancla phaeopteralis** (Guenée).

*Botys phaeopteralis* Guenée, Deltoids and Pyralids, 1854, 349.

Range: Cosmopolitan in tropics.

Grassworm. St. Augustine, 8 April, 1946, from larva feeding on Java grass (*Polytrias praemorsa*) and Savanna grass (*Axonopus compressus*), E. McC. Callan (det. Carl Heinrich).

**Lamprosema indicata** (Fabricius).

*Phalaena indicata* Fab., Syst. Ent., 3, (2), p. 218.

Range: Cosmopolitan.

Bean Leaf-webber. The larva feeds on the leaves of beans, webbing them together. Collected by H. A. Ballou.

**Lamprosema olivia** (Butler).

*Botys olivia* Butler, *Proc. Zool. Soc. Lond.*, (1878).

Range: Cuba, Jamaica, Guatemala, Venezuela, Brazil.

Palmiste, 11 Dec., 1937 (N. L.).

**Gonocausta zephyralis** Lederer.

Lederer, *Wien. Ent. Mon.*, p. 436, t. 17, fig. 5, (1863).

Range: Amboina (type locality), Mexico, Guatemala, Costa Rica, Panama, Colombia, French Guiana.

### Family Pterophoridae.

**Platyptilia** sp.

Brasso, 31 Oct., 1941, from larva eating flush leaves of cacao (*Theobroma cacao*), E. McC. Callan (det. Carl Heinrich).

### Family Carposinidae.

**Carposina bullata** Meyrick.

Meyrick, Exot. Microlep., I, p. 98 (1913).

Range: British Guiana.

The larva feeds within the seed capsule of the weed, *Clidemia hirta* (Parry-Jones, E. & Squire, F. The biological control of *Clidemia hirta*. Dissertation, I. C. T. A., 1931).

### Family Phaloniidae.

**Phalonia** sp.

St. Augustine, 1945, from larva feeding on inflorescences of *Cordia macrostachya*. R. G. Donald (det. Carl Heinrich).

### Family Olethreutidae.

**Gymnandrosoma** sp.

Rio Claro, 23 Feb., 1944, from larva boring in cacao pod (*Throbroma cacao*), A. F. Posnette (det. Carl Heinrich).

**Laspeyresia** sp., near **rhodaspis** Meyrick.

Recorded by Pickles (*Rept. of Entomologist* for 1938, Dept. Agric. Trin. and Tob.) as causing injury to grapefruit and oranges.

### Family Plutellidae.

**Plutella maculipennis** (Curtis).

Curtis, *Brit. Ent.*, pl. 420 (1832).

Range: Cosmopolitan.

Diamond-back moth. A notorious and widely distributed pest of cabbages, cauliflowers and related plants. San Juan, March, 1945, from larva feeding on cabbage leaves, E. McC. Callan (det. Carl Heinrich).

### Family Cosmopterygidae.

**Mompha trithalama** Meyrick.

Meyrick, Exot. Microlep., 2, p. 578 (1922).

Range: Amazon region of Brazil and Peru.

The larva feeds within the seed capsule of the weed, *Clidemia hirta* (Parry-Jones, E. & Squire, F. The biological control of *Clidemia hirta*. Dissertation I. C. T. A., 1931).

### Family Gelechiidae.

**Pectinophora gossypiella** (Saunders).

Saunders, *Trans. Ent. Soc. Lond.*, (1), 3, p. 284 (1843).

Range: Cotton-growing areas.

The pink bollworm of cotton was accidently introduced to Trinidad some 20 years ago.

**Gnorimoschema gudmannella** Walsingham.

Walsingham, *Proc. Zool. Soc. Lond.*, p. 77 (1897).

Range: West Indies.

Pepper flower-bud moth. San Juan, April, 1948, from larva boring in flower-buds of peppers (*Capsicum* spp.), E. McC. Callan.

**Sitatroga cerealella** (Olivier).

Olivier, Encycl. Meth. Ent., 4, p. 121, pl. 46, fig. 8 (1789).

Range: World wide.

St. Augustine, 4 Aug., 1938, from seeds of sorghum (*Sorghum vulgare*), E. McC. Callan. The Angoumois grain moth is a serious pest of many stored grains in Trinidad.

**Epithectis sphecophila** Meyrick.

Meyrick, Exot. Microlep., 4, p. 624 (1936).
Range: Trinidad.
Recorded by Vesey-Fitzgerald (*Trans. Roy. Ent. Soc. Lond.*, 87, 1938, p. 182-3) as a scavenger in nests of *Polistes*.

### FAMILY STENOMIDAE.

**Cerconota anonella** (Sepp).

Sepp, Surinam Vlinders, 3, p. 297, pl. 137 (1830).
Range: Central and South America and West Indies.
A pest of Soursop (see R. G. Fennah, *Trop. Agriculture*, 14, 1937, p. 175).

**Stenoma nitens** Butler.

Butler, *Cistula Entomol.*, 12, p. 188 (1882).
Range: British Guiana, Amazonia.
Palmiste, 22 Nov., 1937 (N. L.).

### FAMILY GRACILARIIDAE.

**Marmara** sp.

Cacao pod miner. The larva mines in the epidermis of cacao pods, causing conspicuous serpentine mines.

### FAMILY TINEIDAE.

**Telphusa latebricola** Meyrick.

Meyrick, Exot. Microlep., 4, p. 349 (1932).
Range: Virgin Islands.
Recorded by Vesey-Fitzgerald (*Trans. Roy. Ent. Soc. Lond.*, 87, 1938, p. 182) as an important enemy of *Polistes canadensis* (L.), the caterpillars feeding as scavengers but also devouring living wasp pupae.

**Leucoptera coffeella** Guérin-Meneville.

Guérin-Meneville & Perrottet, Mem. Ins. Champ. Rav. Cafiers Ant., pp. 5-32, pl. 1, 2 (1842).
Range: Central and South America, Ceylon, West Indies.
The coffee leaf-miner is not uncommon in Trinidad, though damage to the crop is negligible.

**Holophractis heptachaica** Meyrick.

Meyrick, Exot. Microlep., 2, p. 326 (1920).
Range: Brazil: Obidos, Parintins.
Recorded by Meyrick (Exot. Microlep., 4, pt. 1, 1930) as bred from larvae feeding externally on seeds of *Clidemia hirta*.

**Dictomeris granivora** Meyrick.

Meyrick, Exot. Microlep., 4, p. 201 (1932).
Range: Peru, Brazil.
Described from specimen reared from larva in young maize.

**Tineola bisselliella** Hummel.

Hummel, Ess. Ent. 13, (1829).
Range: Europe and North America.
Clothes moth.

**Tinea pellionella** (Linnaeus).

Linnaeus, Syst. Nat., p. 536 (1758).
Range: Universal.
Case-bearing clothes moth.

### FAMILY ACROLOPHIDAE.

**Acrolophus ductifera** Meyrick.

Meyrick, Exot. Microlep., 3, p. 329 (1927).
Range: Antigua.
Collected by H. A. Ballou.

# 18.

# The Euchromiidae (Moths) of Kartabo, British Guiana, and Caripito, Venezuela.[1]

HENRY FLEMING.

*Entomologist, Department of Tropical Research, New York Zoological Society.*

[This contribution is the result of various expeditions of the Department of Tropical Research of the New York Zoological Society to British Guiana and to Venezuela, all under the direction of Dr. William Beebe. The Guiana expeditions were made during the years 1917, 1919, 1920, 1921 and 1924. The expeditions were arranged so that each month of the year is represented in the collections. The Venezuelan expedition in 1942, during which field work was carried on from February 19 to September 2, was sponsored by grants from the Committee for Inter-American Artistic and Intellectual Relations and from four trustees of the Zoological Society, George C. Clark, Childs Frick, Laurance S. Rockefeller and the late Herbert L. Satterlee, and by invaluable assistance from the Standard Oil Companies of New Jersey and Venezuela.]

This is the fourth of a series of papers on the Lepidoptera collected at Kartabo, British Guiana, and Caripito, State of Monagas, Venezuela, by expeditions of the Department of Tropical Research of the New York Zoological Society.

A total of 77 species of Euchromiidae are listed from Kartabo and 44 from Caripito. Although the two localities are approximately 400 miles apart, only 15 species are common to both.

A list of species of Euchromiidae collected in eastern Venezuela by P. Anduze (*Bol. Soc. Ven. Cien. Nat.*, IV, No. 32, p. 307: 1938) records 24 species from Caripito. Anduze's specimens were named by R. Lichy who later published additional notes on this material (*Bol. Soc. Ven. Cien. Nat.* VIII, No. 55, pp. 227-232: 1943). The above two papers list 26 species from Caripito of which 16 species were not taken by us. With our 44 species the total known species from Caripito total 60.

Trinidad (Port-of-Spain) is only 114 miles to the northeast of Caripito. Kaye & Lamont list 83 species from Trinidad (Cat. Trin. Lep. Het. in Mem. Dept. Agric. Trin. Tob., No. 3: 1927). However, in spite of its proximity only 18 species are in common with our list and an additional 7 from Anduze and Lichy's list. In other words approximately 1/3 of the species of Trinidad are in common with Caripito.

As mentioned before, Kartabo and Caripito have 15 species in common. Anduze and Lichy record an additional three species common to both localities. Thus, less than ¼ of the species from Kartabo are common to Caripito.

Only 7 species are common to the three localities.

Two facts are startling; first, that Anduze and ourselves captured so few species at Caripito in common, secondly, that two other comparatively near localities show so little in common.

Since so few species are common to both Kartabo and Caripito, the paper has been divided into two parts so that anyone interested in Kartabo or Caripito separately may refer to the respective part: Part I, The Euchromiidae of Kartabo, p. 209; and Part II, The Euchromiidae of Caripito, p. 214.

For maps and a detailed account of the ecology of Kartabo and Caripito, see Beebe, "Studies of a Tropical Jungle: One Quarter of a Square Mile of Jungle at Kartabo, British Guiana," *Zoologica*, Vol. VI, pp. 1-193 (1925), and "Physical Factors in the Ecology of Caripito, Venezuela," *Zoologica*, Vol. XXVIII, pp. 53-59 (1943).

One new species is described from Caripito. The holotype and allotype have been deposited in the collection of the American Museum of Natural History. One paratype is in the collection of the Department of Tropical Research.

## PART I.

### THE EUCHROMIIDAE OF KARTABO, BRITISH GUIANA.

**Pompilopsis tarsalis** (Walker).

Walker, List Lep. Ins. Br. Mus., 1, p. 196, (1854). (*Glaucopis*).

Two specimens, one on April 12 flying in the forest about noontime and the other taken on June 21 on the bark of a tree.

Range: Mexico to the Amazons. A new record for British Guiana.

**Pompiliodes tenebrosa** (Walker).

Walker, List Lep. Ins. Br. Mus., 1, p. 240, (1854). (*Euchromia*).

One specimen on December 8.

Range: Reported from the lower Amazon. A new record for British Guiana.

**Isanthrene crabroniformis crabroniformis** Staudinger.

Staudinger, *Verh. zool.-bot. Ges. Wien*, 25, p. 120, (1875).

One specimen on February 16.

[1] Contribution No. 883, Department of Tropical Research, New York Zoological Society.

Range: Costa Rica to Venezuela. This species subspeciates in Venezuela, but the British Guiana specimen before me appears to be the typical *c. crabroniformis*. A new record for British Guiana.

**Isanthrene melaena** (Cramer).

Cramer, Pap. Exot. 1, p. 71, t. 45, fig. G, (1775). (*Sphinx melas*).

One specimen without a date.

Range: Surinam to Paraguay. A new record for British Guiana.

**Isanthrene varia** (Walker).

Walker, List. Lep. Ins. Br. Mus., 1, p. 157, (1854). (*Glaucopis*).

One specimen on February 1.

Range: Amazons to Rio de Janeiro. A new record for British Guiana.

**Isanthrene porphyria** (Walker).

Walker, List Lep. Ins. Br. Mus., 1, p. 157, (1854). (*Glaucopis*).

One specimen without a date.

Range: Surinam, Amazon region and Peru. A new record for British Guiana.

**Hyda basilutea** (Walker).

Walker, List. Lep. Ins. Br. Mus., 1, p. 182, (1854). (*Glaucopis*).

Two specimens, April 4 and May 5.

Range: Colombia to Brazil. A new record for British Guiana.

**Autochloris vitristriga** Druce.

Druce, *Ann. & Mag. Nat. Hist.*, (6), 20, p. 301, (1897).

One specimen without a date.

Range: Venezuela, British and French Guiana.

**Phoenicoprocta vacillans** (Walker).

Walker, List. Lep. Ins. Br. Mus., 7, p. 1617, (1856). (*Eunomia*).

One female without a date.

Range: Northern South America to Bolivia and southern Brazil. A new record for British Guiana.

**Pheia xanthozona** Dognin.

Dognin, Hét. Nouv. Am. Sud., 1, p. 3, (1910).

Two specimens, one on December 11 and the other without a date.

Range: Described from French Guiana. A new record for British Guiana.

**Loxophlebia splendens** Möschler.

Möschler, *Stett. Ent. Zeitg.*, 33, p. 345, (1872). (*Chrysostola*).

Four specimens: April 3, August 12, October 12 and November 4.

Range: Described from Surinam. A new record for British Guiana.

**Loxophlebia geminata** Schaus.

Schaus, *Proc. U. S. Nat. Mus.*, 29, p. 185, (1905).

Two specimens: one on January 16 and the other without a date.

Range: Described from French Guiana. A new record for British Guiana.

**Mesothen nana** Schaus.

Schaus, *Proc. U. S. Nat. Mus.*, 29, p. 185, (1905).

Five specimens: one on July 4 and the remainder in November.

Range: Described from Surinam. A new record for British Guiana.

**Chrostosoma decisa** (Walker).

Walker, List Lep. Ins. Br. Mus., 31, p. 81, (1864). (*Pseudomya*).

Three specimens: January 16, April 1 and June 6.

Range: Amazons and Bolivia. A new record for British Guiana.

**Chrostosoma echemus** (Cramer).

Cramer, Pap. Exot., 4, p. 147, t. 367, fig. B, (1782). (*Sphinx*).

Five specimens: one October 27 and the other four specimens without dates. This species is not clearly defined. The specimens above agree with Walker's description of *dolens*. Hampson synonomized Walker's name under *echemus*, which has a red head. On the other hand, our specimens have a brown head.

Range: Panama to south Brazil. A new record for British Guiana.

**Leucotmemis varipes** (Walker).

Walker, List Lep. Ins. Br. Mus., 1, p. 175, (1854). (*Glaucopis*).

Four specimens: March 9, April 16, May and one with no date.

Range: Amazon region. A new record for British Guiana.

**Leucotmemis lemoulti** (Rothschild).

Rothschild, *Novit. Zool.*, 18, p. 156, (1911). (*Cosmosoma*).

One specimen on July 23.

Range: Described from French Guiana. A new record for British Guiana.

**Cosmosoma metallescens** (Ménétries).

Ménétries, Cat. Lép. Pétersb., 2, p. 138, t. 14, f. 1, (1857). (*Laemocharis*).

One specimen on March 27.

Range: Mexico to the Amazons.

**Cosmosoma xanthostictum** Hampson.

Hampson, Cat. Lep. Phal., 1, p. 240, t. 9, f. 21, (1898).

One specimen on June 10.

Range: Mexico to Panama. A new record for British Guiana.

**Cosmosoma oratha** (Druce).

Druce, *Proc. Zool. Soc. Lond.*, p. 281, (1893). (*Autochloris*).

Three specimens: March 12, May 16 and December 31.

Range: Described from British Guiana.

**Cosmosoma nelea** Möschler.

Möschler, *Verh. zool.-bot. Ges. Wien*, 27, p. 635, t. 8, f. 4, (1877).

One specimen taken on June 20.

Range: Surinam. A new record for British Guiana.

**Poecilosoma chrysis** Hübner.

Hübner, Zutr. Exot. Schmett., 2, p. 8, f. 211, 212, (1827).

One reared specimen with the following account from Dr. William Beebe's field notes.

"A single specimen of caterpillar found on July 28 at the side of the road at Camaria, in the middle of the leaf of a species of Moriaciae.

"Description: Length 25 mm.; form cylindrical, each segment somewhat swollen centrally. Body slightly smaller posteriorly and anteriorly than in the middle. General color white, becoming slightly yellower on the thoracic segments. Head empire yellow. True legs pinard yellow, the anal and prolegs somewhat paler. The greater part of the body covered with white hairs, the hairs being set in small tufts, and measuring 4 to 5 mm. in length. On the first and eighth abdominal segments there is on each side a very stout group of these hairs, these groups very conspicuous. The eighth abdominal segment carries four long (10 mm.) dark hairs tipped with white. Two of them extend almost vertically, while the other two extend laterally.

"July 29. The entire coloration has changed to chalcedony yellow, and the four long hairs have entirely disappeared.

"July 30. Caterpillar has spun its cocoon. The cocoon is shaped like the egg of a snake or lizard. It is attached to the side of the terrarium by its side, and one can look directly within it. Length of cocoon 22 mm., width 14 mm. Cocoon dull marguerite yellow, very finely spun and intermeshed. The outside is covered with the chalcedony hairs of the caterpillar, which are laid flat about the pupal case and meshed into each other. A number of these yellow hairs are scattered promiscuously over the surface of the glass. A few black hairs, also covered with short branches, scattered meagerly over the surface. These hairs have the branches much more plentiful at the tip. General color of pupa: wings, thorax and head glass green; abdominal segments white with a greenish tinge; line down central portion of dorsal abdominal segments glass green; spiracles and a spot near the base of the wing dark brown. Pupa entirely naked. The caterpillar's skin is present within the cocoon, attached loosely to the abdominal end of the pupa.

"August 8. Pupa hatched. See specimen No. 2096 and pupa case No. 2097."

**Mystrocneme varipes** (Walker).

Walker, List Lep. Ins. Br. Mus., 1, p. 235, (1854). (*Euchromia*).

Four specimens: January 4, November 22, December 8 and one without a date.

Range: Venezuela, French Guiana and Amazons. A new record for British Guiana.

**Ichoria chrastosomides** Schaus.

Schaus, *Proc. U. S. Nat. Mus.*, 29, p. 187, (1905).

One specimen without a date.

Range: French Guiana. A new record for British Guiana.

**Pseudomya picta** Schaus.

Schaus, *Proc. Zool. Soc. Lond.*, p. 226, (1894).

Three specimens: February 24, April 2 and August 23.

Range: Venezuela and Guianas.

**Pseudomya melanthus** (Stoll).

Stoll in Cramer, Pap. Exot., 4, p. 147, t. 367, f. C, (1782). (*Sphinx*).

Three specimens: May 26 (2) and November 11.

Range: Colombia, Surinam and Brazil. A new record for British Guiana.

**Saurita cassandra** (Linnaeus).

Linnaeus, Syst. Nat., ed. 10, p. 494, (1758). (*Sphinx*).

Seven specimens: Jan. 14, April 1, 2, May 15, September 1 and two without a date.

Range: Widely distributed in South America but never reported specifically from British Guiana.

**Saurita incerta** (Walker).

Walker, List Lep. Ins. Br. Mus., 7, p. 1627, (1856). (*Tipulodes*).

Two specimens on April 29.

Range: Panama and Colombia. A new record for British Guiana.

**Saurita afflicta** (Walker).

Walker, List. Lep. Ins. Br. Mus., 1, p. 144, (1854). (*Glaucopis*).

Five specimens: March 3, October 16 and 3 without dates.

Range: Honduras to the Amazons. A new record for British Guiana.

**Saurita tipulina** (Hübner).

Hübner, Samml. Exot. Schmett., 1, t. 163, (1827). (*Glaucopis*).

Four specimens: March, August 22, September 20 and one with no date.

Range: Widely distributed from Mexico to South Brazil but not previously reported from British Guiana.

**Dycladia lucetius** (Stoll).

Stoll in Cramer, Pap. Exot., 4, p. 129, t. 357, f. D, (1782). (*Sphinx*).

One specimen without date.

Range: Para to south Brazil. A new record for British Guiana.

**Syntomeida melanthus** (Cramer).

Cramer, Pap. Exot., 3, p. 94, t. 248, f. C, (1780). (*Sphinx*).

One specimen without date.

Range: Mexico to Uruguay and Peru. This is the first record from British Guiana.

**Histiaea cephus** (Cramer).

Cramer, Pap. Exot. 3, t. 197, f. E, (1779). (*Sphinx*).

Two specimens: December 10 and #10.

Range: Trinidad, Venezuela and Surinam. A new record for British Guiana.

**Calonotus helymus** (Cramer).

Cramer, Pap. Exot., 1, p. 4, t. 2, f. D, E, (1775). (*Sphinx*).

Three specimens: March 30 (2) and no date.

Range: French Guiana. A new record for British Guiana.

**Trichura cerberus** (Pallas).

Pallas, Spic. Zool., 9, p. 27, t. 2, f. 8, (1772). (*Sphinx*).

Two specimens: no dates.

Range: Venezuela and Trinidad through Surinam to south Brazil.

**Cormatura aliaria** (Druce).

Druce, *Proc. Zool. Soc. Lond.*, p. 494, t. 42, f. 3, (1890). (*Trichura*).

Three specimens: August 3, no date (2).

Range: French Guiana to Brazil. A new record for British Guiana.

**Aethria aner** Hampson.

Hampson, *Ann. & Mag. Nat. Hist.*, (7), 15, p. 428, (1905).

One specimen: March 17.

Range: Venezuela and French Guiana. A new record for British Guiana.

**Aethria leucaspis** (Cramer).

Cramer, Pap. Exot., 1, p. 83, t. 52, f. C, D, (1775). (*Sphinx*).

Three specimens: June 4 and two without dates.

Range: Venezuela, Surinam, British and French Guiana, Brazil and Bolivia.

**Hypocladia parcipuncta** Hampson.

Hampson, *Ann. & Mag. Nat. Hist.*, (8), 4, p. 347, (1909).

One specimen without a date.

Range: Described from British Guiana.

**Eumenogaster haemacera** Hampson.

Hampson, Cat. Lep. Phal., 1, p. 369, t. 13, f. 1, (1898).

One specimen on April 12.

Range: Venezuela, Guianas and the Amazon region.

**Urolasia brodea** (Schaus).

Schaus, *Jour. N. Y. Ent. Soc.*, 4, p. 132, (1896). (*Syntrichura*).

One specimen on August 9.

Range: Trinidad. A new record for British Guiana.

**Cercopimorpha homopteridea** Butler.

Butler, *Jour. Linn. Soc. Lond.*, Zool. 12, p. 424, (1876).

Three specimens: March 3, 7 and 26.

Range: Para. A new record for British Guiana.

**Episcepsis melanitis** (Hübner).

Hübner, Zutr. Exot. Schmett., 1, p. 19, f. 93, 94, (1827). (*Centronia*).

One specimen on January 4.

Range: British and French Guiana.

**Episcepsis lenaeus** (Cramer).

Cramer, Pap. Exot., 3, p. 95, t. 248, f. G, (1780). (*Sphinx*).

One specimen on April 17.

Range: Mexico through Central America to British Guiana and Surinam.

**Episcepsis gnoma** (Butler).

Butler, Illustra. Het. Br. Mus., 1, p. 44, t. 16, f. 2, (1877). (*Heliura*).

Thirteen specimens: January 12, February 7, 24, March 3, July 16, August 12, September 14 and six without a date.

Range: French Guiana, Amazons to south Brazil. A new record for British Guiana.

**Episcepsis redunda** Schaus.

Schaus, *Ann. & Mag. Nat. Hist.*, (8), 6, p. 190, (1910).

Five specimens: April 2, June 6, 10, August 11 and one without a date.

Range: Mexico through Central America to Guianas and Peru.

**Ceramidia phemonoides** (Möschler).

Möschler, *Verh. zool.-bot. Ges. Wien*, 27, p. 639, t. 8, f. 10a, (1854). (*Antichloris*).

Two specimens without dates.

Range: Venezuela, Guianas and Amazons.

**Ceramidia chloroplegia** (Druce).

Druce, *Ann. & Mag. Nat. Hist.*, (7), 15, p. 462, (1905).

One specimen without a date.

Range: Venezuela and French Guiana. A new record for British Guiana.

**Androcharta diversipennis** (Walker).

Walker, List Lep. Ins. Br. Mus., 1, p. 225, (1854). (*Euchromia*).

Two specimens without dates.

Range: Venezuela, Amazons and Peru. A new record for British Guiana.

**Antichloris eriphia** (Fabricius).

Fabricius, Gen. Ins., p. 276, (1776). (*Zygaena*).

Two specimens: April 2, no date.

Range: Venezuela and Trinidad to Paraguay and Bolivia.

**Atyphopsis modesta** Butler.

Butler, *Trans. Ent. Soc. Lond.*, p. 49, (1878).

Four specimens: May 6, October 20 and two without dates.

Range: Guianas and Amazons.

**Napata leucotela** Butler.

Butler, *Journ. Linn. Soc. Lond.*, Zool. 12, p. 409, (1876).

One specimen on May 16.

Range: Mexico through Central America to Venezuela and Surinam. A new record for British Guiana.

**Xanthopleura perspicus** (Walker).

Walker, List Lep. Ins. Br. Mus., 7, p. 1627, (1856). (*Calonotus*).

One specimen without a date.

Range: Colombia, Ecuador, Peru and the Amazons. A new record for British Guiana.

**Cacostatia ossa** (Druce).

Druce, *Proc. Zool. Soc. Lond.*, p. 285, (1893). (*Metastatia*).

One specimen on March 2.

Range: Panama, Colombia and the Guianas.

**Aclytia gynamorpha** Hampson.

Hampson, Cat. Lep. Phal. 1, p. 457, (1898).

Nine specimens: June 4, 5, 8, 16, Oct. 14 and four specimens without dates.

Range: French Guiana and the Amazons. A new record for British Guiana.

**Aclytia heber** (Cramer).

Cramer, Pap. Exot., 3, pl. 287, A, (1780), (*Sphinx*).

Five specimens: May 11, June 16, August 17, December 8 and no date.

Range: Widely distributed throughout the American tropics from Mexico and Cuba to south Brazil. The undated specimen listed above agrees with Draudt's abberation *insignata* described from Mexico.

**Aclytia bractea** (Möschler).

Möschler, *Verh. zool.-bot. Ges. Wien*, 27, p. 645, t. 8, f. 15, (1877). (*Sciopsyche*).

One specimen on May 1.

Range: Surinam. A new record for British Guiana.

**Euagra caelestina** (Stoll).

Stoll in Cramer, Pap. Exot., 4, p. 107, t. 345, f. 9, (1782). (*Bombyx*).

Four specimens: January 16, February 28, October 1 and one without a date.

Range: French Guiana and the Amazons. A new record for British Guiana.

**Agyrta micilia** (Cramer).

Cramer, Pap. Exot., 3, p. 62, t. 228, f. G, (1780). (*Bombyx*).

Three specimens: August 12 and two without dates.

Range: Panama, Venezuela, Surinam, French Guiana, Amazons and Ecuador. A new record for British Guiana.

**Delphyre hebes** Walker.

Walker, List Lep. Ins. Br. Mus., 2, p. 537, (1854).

Three specimens: June 26, July 17 and one without a date.

Range: Described from Honduras. A new record for British Guiana.

**Delphyre aclytioides** Hampson.

Hampson, *Ann. & Mag. Nat. Hist.*, (7), 8, p. 174, (1901).

One specimen on June 24.

Range: French Guiana. A new record for British Guiana.

**Delphyre dizona** (Druce).

Druce, *Ann. & Mag. Nat. Hist.*, (7), 1, p. 406, (1898). (*Neacerea*).

Two specimens: June 11 and August 5.

Range: French Guiana. A new record for British Guiana.

**Heliura suffusa** (Lathy).

Lathy, *The Ent.*, 32, p. 120, (1899). (*Neacerea*).

Two specimens: April 2 and no date.

Range: French Guiana to south Brazil. A new record for British Guiana.

**Heliura rhodophila** (Walker).

Walker, List Lep. Ins. Br. Mus., 7, p. 1638, (1856). (*Eucerea*).

One specimen on May 29.

Range: Honduras to the Amazons.

**Heliura zonata** Druce.

Druce, *Ann. & Mag. Nat. Hist.*, (7), 15, p. 464, (1905).

Two specimens: May 2 and July 9.

Range: Venezuela and British Guiana.

**Eucereum flavum** Dognin.

Dognin, Het. Nouv. Am. Sud., 1, p. 6, (1910).

One specimen on March 6.

Range: French Guiana. A new record for British Guiana.

**Eucereum maricum** (Cramer).

Cramer, Pap. Exot., 1, pl. 20, f. F, G, (1775). (*Sphinx*).

Four specimens: June 12, July 9, September 25 and October 10. The specimen captured on September 25 is referable to Rothschild's *E. postcoerulem* (*Novit. Zool.*, 19, p. 171, 1912). However, while there are only four specimens before me, there is a strong indication that the width of the dark margin of the hindwing is only an individual variation. The disc of the hindwing also varies between nile blue and bluish white. The postdiscal band of the forewing is also variable in width.

Range: British Guiana through Venezuela as far as Bolivia.

**Eucereum hyalium** Kaye.

Kaye, *Trans. Ent. Soc. Lond.*, p. 119, t. 5, f. 11, (1901).

Four specimens: March 18, May 16, June 24 and December 8.

Range: Trinidad and British Guiana.

**Eucereum latifascia** Walker.

Walker, List Lep. Ins. Br. Mus., 7, p. 1639, (1856).

Three specimens: July 7, December 8 and no date.

Range: Mexico to the Amazons and Peru.

**Eucereum xanthurum** Schaus.

Schaus, *Ann. & Mag. Nat. Hist.*, (8), 6, p. 192, (1910).

One unusually small specimen on July 17.

Range: Mexico, Costa Rica and Brazil. A new record for British Guiana.

**Eucereum marmoratum** Butler.

Butler, Illustr. Het. Br. Mus., 1, p. 50, t. 16, f. 4, (1877).

Two specimens: no dates.

Range: Venezuela to the Amazons.

**Eucereum theophanes** Schaus.

Schaus, *Proc. U. S. Nat. Mus.*, 65, Art. 7, p. 17, (1924).

One specimen: July 17.

Range: Described from British Guiana.

**Correbia lycoides** (Walker).

Walker, List Lep. Ins. Br. Mus., 1, p. 256, (1854). (*Euchromia*).

One specimen: no date.

Range: Mexico to Paraguay, also Cuba and Jamaica, but not previously reported from British Guiana.

**Correbia tristitia** Kaye.

Kaye, *The Ent.*, 44, p. 145, (1911).

One specimen: no date.

Range: British Guiana.

**Correbidia calopteridia** (Butler).

Butler, *Proc. Zool. Soc. Lond.*, p. 381, (1878). (*Pionia*).

One specimen: no date.

Range: French Guiana, Para and Peru. A new record for British Guiana.

**Ctenucha circe** (Stoll).

Stoll in Cramer, Pap. Exot., 3, p. 124, 147, t. 263, f. D, t. 274, f. E, (1780). (*Bombyx*).

Two specimens: May 26 and June 15.

Range: Nicaragua to Ecuador, Venezuela to Brazil but not previously reported from British Guiana.

**Hyaleucerea fusiformis** (Walker).

Walker, List Lep. Ins. Br. Mus., 7, p. 1629, (1856). (*Pampa*).

One specimen on August 12.

Range: French Guiana to the Amazons. A new record for British Guiana.

## PART II.

## THE EUCHROMIIDAE OF CARIPITO, VENEZUELA.

**Isanthrene crabroniformis venezuelana** Draudt.

Draudt in Seitz, *Macrolep. World*, 6, p. 47, (1915).

One specimen on June 30.

Range: Distributed from Costa Rica to British Guiana with this subspecies thus far restricted to Venezuela.

**Hyda basilutea** (Walker).

Walker, List Lep. Ins. Br. Mus., 1, p. 182, (1854). (*Glaucopis*).

Three specimens: March 15, May 16 and July 23.

Range: Colombia to Brazil.

**Autochloris completa?** (Walker).

Walker, List Lep. Ins. Br. Mus., 1, p. 153, (1854). (*Glaucopis*).

Two specimens on March 23. The identification is uncertain because the abdomen of one of the specimens is missing and the abdomen of the other is greasy.

Range: Amazons and Peru. A new record for Venezuela.

**Autochloris umbratus**, new species.

Length of forewing of male 17-18 mm., of female 20 mm.

Pattern of fore and hindwings similar to that of *Autochloris suffumata* Draudt (Draudt in Seitz, *Macrolep. World*, 6, p. 52, pl. 11e, 1915), but with the hyaline areas even further reduced.

Head brown with the exception of a few scattered long white scales on the dorsal anterior margin of the eye and a metallic blue spot on the dorsum at the extreme caudal part of the head. Palpi brown, upturned, with some long porrect scales on the first segment. Antennae bipectinate, gradually broadening to the middle segments and then narrowing again.

Thorax brown, each collar lappet with a metallic blue spot but the shoulder lappets concolorous brown. Just below the collar lappets a more or less quadrilateral white spot. The meso and metathorax have similar spots just lateral of the median ventrum. These latter spots are usually covered by the legs. The legs are brown except the whole anterior side of the fore coxae and the distal tips of the anterior side of the remaining coxae are white.

The first abdominal segment of the male is creamy white. In the female the first abdominal segment is blackish-brown with metallic green dorsolateral spots. The remainder of the abdominal segments of our female are rubbed but appear to be similar in pattern to the male. A median dorsal line of blue or greenish-blue spots from the second abdominal segment to, but not including, the last abdominal segment. A dorsolateral series of blue or greenish-blue streaks on the anterior portion of each segment and a brick red streak on the posterior portion of each of the same segments except the first and last segment. The last segment is concolorous brick red. In the male the ventrum is brown with three lateral ventral spots on the third, fourth and fifth segments. In the female the ventrum is similarly brown, but there are four ventral lateral spots which are so much larger than they are in the male that they form a line rather than a series of spots. The line commences on the second abdominal segment and ends on the fifth.

Forewings of male and female similar except for the larger size of the female wings. The discal cell of the forewing hyaline except for the outer 2 mm. The upper ⅔, or the part of the cell $Cu_2$ above the anal fold, hyaline as far out as vein $Cu_2$. Small hyaline spots having one edge lying on the margin of the discal cell in cells $Cu_1$, $M_3$ and $M_2$. A small spot at base of vein $R_{3+4+5}$. In the holotype this spot is very faint but distinct in the other two types. Hyaline above subcostal vein near base. Line of dark scales resembling a vein running through middle of cell. Remainder of wing brownish-black.

Hindwings of the two sexes similar. Outer and inner margins of the hindwings broadly bordered blackish-brown. This band is 2 mm. wide in the cubital region. Costal region above the discal cell and $R_s$ blackish-brown. Region between discal cell end and outer margin band and between discal cell and vein $A_2$ hyaline.

This species is very similar to *A. suffumata* Draudt (*loc. cit.*) described from one female captured at Medina, Colombia. The wing pattern of *umbratus* differs in the reduction of the hyaline areas. For instance, the dark brown intrudes within the discal cell for 2 mm. and the hyaline areas outside the lower part of the discal cell are smaller and appear as three spots in *umbratus*. In the hindwing the hyaline area is reduced by the band around the margins of the wings being wider in *umbratus*. The forehead of *umbratus* is not white. When Draudt writes of the forehips being white, I interpret it as the coxae of the prothoracic legs. In which case *umbratus* differs from *suffumata* in that one side of the coxae of all six legs is white in *umbratus*. In the description of *suffumata* no mention is made of the median dorsal line of blue spots on the abdomen present in *umbratus*. Neither is any mention made of the brick red dorso-lateral scales on the caudal side of the abdominal segments present in *umbratus*. Draudt mentions "a sub-

lateral row of yellow red spots." These are presumably the spots on the ventrum of *umbratus* which are white.

Material: Holotype, male No. 42492, Caripito, Venezuela; April 7. Allotype, female No. 42493, Caripito, Venezuela; March 30. Paratype, male No. 42494, Caripito, Venezuela; April 29.

**Phoenicoprocta vacillans** (Walker).

Walker, List Lep. Ins. Br. Mus., 7, p. 1617, (1856). (*Eunomia*).

Three specimens: June 15, June 19 and July 11.

Range: Venezuela to Brazil and Bolivia.

**Chrostosoma decisa** (Walker).

Walker, List Lep. Ins. Br. Mus., 31, p. 81, (1864). (*Pseudomya*).

Ten specimens: March 16, April 3, 7, 21 (2), 27, 29, May 1, June 2, 3.

Range: Amazons and Bolivia. A new record for Venezuela.

**Chrostosoma echemus** (Cramer).

Cramer, Pap. Exot., 4, p. 147, t. 367, f. B, (1782). (*Sphinx*).

Seven specimens: March 11, 20 (2), 23, 26 (2) and June 3. These specimens have a dark brown head like the Kartabo, British Guiana, specimens.

Range: Panama to south Brazil.

**Cosmosoma auge** (Linnaeus).

Linnaeus, Syst. Nat., ed. 12, i (2), p. 807, (1767). (*Sphinx*).

One specimen on July 7.

Range: Widely distributed from Mexico to Uruguay.

**Cosmosoma teuthras teuthras** (Walker).

Walker, List Lep. Ins. Br. Mus., 1, p. 168, (1854). (*Glaucopis*).

Three specimens: June 3 and July 6 (2).

Range: Mexico to Argentina.

**Cosmosoma telephus** (Walker).

Walker, List Lep. Ins. Br. Mus., 1, p. 170, (1854). (*Glaucopis*).

One specimen on July 7.

Range: Colombia to Argentina.

**Cosmosoma tengyra** (Walker).

Walker, List Lep. Ins. Br. Mus., 1, p. 167, (1854). (*Glaucopis*).

One specimen on May 11.

Range: Para. A new record for Venezuela.

**Rhynchopyga flavicollis** (Druce).

Druce, Biol. Centr. Am. Het., 1, p. 46, t. 7, f. 11, (1884). (*Amycles*).

One specimen on July 7.

Range: Guatemala to Venezuela.

**Saurita salta** (Schaus).

Schaus, *Proc. Zool. Soc. Lond.*, p. 226, (1894). (*Thrinacia*).

One specimen on March 9.

Range: Venezuela.

**Saurita cassandra** (Linnaeus).

Linnaeus, Syst. Nat., ed. 10, p. 494, (1758). (*Sphinx*).

Eight specimens: June 10, 16, 21, July 4, 10, 12 (2) and 28.

Range: Venezuela and Trinidad.

**Saurita afflicta** (Walker).

Walker, List Lep. Ins. Br. Mus., 1, p. 144, (1854). (*Glaucopis*).

Seven specimens: March 5, 9, June 1, July 23, 26, August 23 and 24.

Range: Honduras to the Amazons.

**Saurita tipulina** (Hübner).

Hübner, Samml. Exot. Schmett., 1, t. 163, (1827). (*Glaucopis*).

One female captured on August 23.

Range: Mexico to south Brazil.

**Psoloptera leucosticta** (Hübner).

Hübner, Samml. Exot. Schmett., 1, (1827). (*Glaucopis*).

Sixteen specimens: March 20 (2), 23 (2), April 6 (4), 8, 16, 18, May 8, June 3, July 7 and 27 (2). Common at lights at night and also to be found during the day in open parts of the forest. It runs rapidly about the leaves of low plants, raising and lowering its wings like flies frequently seen in the same location.

Range: Venezuela, Trinidad, Guianas and Amazon region.

**Hystiaea cephus** (Cramer).

Cramer, Pap. Exot., 3, t. 197, f. E, (1779). (*Sphinx*).

Ten specimens: March 13, April 8, 22, 26, May 4 (2), 17, 19, 25 and July 27.

Range: Trinidad, Venezuela, British Guiana and Surinam.

**Hystiaea meldolae** Butler.

Butler, *Journ. Linn. Soc. Lond.*, Zool. 12, p. 362, (1876).

Four specimens: March 6, May 4, 5 and 12.

Range: Panama, Venezuela and Trinidad.

**Macrocneme thyra** Möschler.

Möschler, *Verh. zool.-bot. Ges. Wien*, 32, 334, pl. 18, f. 24, (1883).

Two specimens: April 8 and May 4.

Range: Panama to Peru and Guianas. A new record for Venezuela.

**Macrocneme thyridia** Hampson.

Hampson, Cat. Lep. Phal., 1, 321, pl. 11, f. 9, (1898).

Three specimens: June 3, 12 and August 1.

Range: Honduras to Guianas and Amazons.

**Macrocneme vittata** (Walker).

Walker, List Lep. Ins. Br. Mus., 1, p. 249, (1854).

Six specimens: July 6, 27, August 23 (3) and 24.

Range: Venezuela to Amazons.

**Macrocneme albitarsia** Hampson.

Hampson, Cat. Lep. Phal., 1, p. 325, pl. 12, f. 6, (1898).

One specimen on July 15.

Range: Panama to Amazons.

**Macrocneme nigrotarsia** Hampson.

Hampson, Cat. Lep. Phal., 1, p. 326, pl. 12, f. 24, (1898).

Twelve specimens: April 23, July 5, 27 (2), 30, August 23 (3), 24 (4) and 27 (2).

Range: Mexico to Trinidad.

**Macrocneme** sp.

Two specimens: June 3 and July 1.

**Macrocneme** sp.

One specimen on August 23.

**Calonotus tiburtus** (Cramer).

Cramer, Pap. Exot., 3, p. 75, t. 237, f. C, (1780). (*Sphinx*).

Nine specimens: May 2, 19, June 2, July 1, 2, 6, 27 and August 8 (2).

Range: Costa Rica, Panama to Surinam.

**Calonotus tripunctatus** Druce.

Druce, *Ann. & Mag, Nat. Hist.*, (7), 1, p. 401, (1898).

Two specimens: May 17 and July 16.

Range: Trinidad and St. Vincent. A new record for Venezuela.

**Dinia mena** (Hübner).

Hübner, Samml. Exot. Schmett., 2 (1827). (*Eunomia*).

Nineteen specimens: April 23, July 24, 27 (2), August 15, 21 (5), 23 (8) and 24. A common visitor to the lights at night as well as to the flower *Clibadium surinamense* Linn. during the day.

Range: Panama to Brazil, Peru and Ecuador.

**Aethria andromacha** (Fabricius).

Fabricius, Syst. Ent., p. 830, (1775). (*Zygaena*).

Five specimens: August 23 (2), 24 (2) and 25.

Range: Venezuela, Surinam and Para.

**Syntrichura reba** Druce.

Druce, *Ann. & Mag. Nat. Hist.*, (6), 18, p. 33, (1896).

Three specimens: July 24 and August 23 (2).

Range: Panama, Colombia and Venezuela.

**Episcepsis inornata** (Walker).

Walker, List Lep. Ins. Br. Mus., 7, p. 1636, (1856). (*Automolis*).

One specimen on May 1.

Range: Mexico through Central America to Venezuela.

**Ceramidia phemonoides** (Möschler).

Möschler, *Verh. zool.-bot. Ges. Wien*, 27, p. 639, t. 8, f. 10, 10a, (1854). (*Antichloris*).

Two specimens: April 23 and July 15.

Range: Venezuela, Guianas and Amazon region.

**Ceramidia chloroplegia** Druce.

Druce, *Ann. & Mag. Nat. Hist.*, (7), 15, p. 462, (1905).

Two specimens: July 16 and August 4.

Range: Venezuela, British and French Guiana.

**Amycles affinis** Rothschild.

Rothschild, *Novit. Zool.*, 19, p. 153, (1912).

One specimen with no date.

Range: Mexico to Venezuela.

**Napata leucotela** Butler.

Butler, *Journ. Linn. Soc. Lond.*, Zool. 12, p. 409, (1876).

Eleven specimens: February 23, March 27, April 23, June 3, July 3, 24, 26, August 23, 24 (2) and 27. Not taken at the lights at all but common about the flower of *Clibadium surinamense* Linn.

Range: Mexico through Central America and northern South America to Surinam.

**Horama panthalon** (Fabricius).

Fabricus, Syst. Ent., p. 405, (1793). (*Zygaena*).

Twenty-one specimens: March 15 (4), June 3 (5), 7, 13 and 15 (10).

Range: Reported from Haiti and Venezuela.

**Ixylasia** sp.

A female in very poor condition which seems to resemble *I. trogonoides*, recorded from Brazil, rather than *I. pyroproctis* from Venezuela. Specimen was captured on April 15.

**Agyrta dux** (Walker).

Walker, List Lep. Ins. Br. Mus., 2, p. 327, (1854). (*Dioptis*).

One specimen on April 6.

Range: Honduras to Venezuela.

**Agyrta micilia** (Cramer).

Cramer, Pap. Exot., 3, p. 62, t. 228, f. G, (1780). (*Bombyx*).

One specimen on March 9.

Range: Panama to Brazil and Ecuador.

**Heliura rhodophila** (Walker).

Walker, List Lep. Ins. Br. Mus., 7, p. 1638, (1856). (*Eucerea*).

Four specimens on July 15.

Range: Honduras to the Amazons.

**Eucereon aeolum** Hampson.

Hampson, Cat. Lep. Phal., 1, p. 498, t. 16, f. 16, (1898).

One specimen on July 27.

Range: Mexico to Venezuela.

**Eucereon punctatum** (Guérin).

Guérin, Icon Règne Animal, Ins., p. 515, (1844). (*Chelonia*).

Two specimens on May 1.

Range: Guatemala to Paraguay.

**Correbia lycoides** (Walker).

Walker, List Lep. Ins. Br. Mus., 1, p. 256, (1854). (*Euchromia*).

One specimen on March 26.

Range: Mexico to Paraguay.

# NEW YORK ZOOLOGICAL SOCIETY

General Office: 30 East Fortieth Street, New York 16, N. Y.
Publication Office: The Zoological Park, New York 60, N. Y.

# ZOOLOGICA

SCIENTIFIC CONTRIBUTIONS

*of the*

NEW YORK ZOOLOGICAL SOCIETY

VOLUME 35

Numbers 19 & 20

Part 4



Published by the Society

The Zoological Park, New York

December 30, 1950

# CONTENTS

# 19.

# Eastern Pacific Expeditions of the New York Zoological Society. XLII. Mollusks from the West Coast of Mexico and Central America. Part IX.[1]

Leo George Hertlein & A. M. Strong.
*California Academy of Sciences.*

(Plates I & II.)

[This is the forty-second of a series of papers dealing with the collections of the Eastern Pacific Expeditions of the New York Zoological Society made under the direction of William Beebe. The present paper is concerned with specimens taken on the Templeton Crocker Expedition (1936) and the Eastern Pacific *Zaca* Expedition (1937-1938). For data on localities, dates, dredges, etc., refer to *Zoologica*, Vol. XXII, No. 2, pp. 33-46, and Vol. XXIII, No. 14. pp. 287-298.]

Contents. Page



## Introduction.

This is the ninth of a series of papers dealing with collections of mollusks taken on the Templeton Crocker Expedition (1936) and the Eastern Pacific *Zaca* Expedition (1937-1938). The general plan of presentation is, in general, that mentioned in Part II of this series of papers.[2] Formal headings and keys are given only for the species collected by the Expeditions of 1936 and 1937-1938. Occasionally additional species are included in the keys for convenience but in such cases it is indicated which ones do not occur in the present collections. The present paper completes the work dealing with the Pelecypoda.

Acknowledgment is due Dr. G. D. Hanna, Curator, Department of Paleontology of the California Academy of Sciences, and Mr. A. G. Smith, Research Associate of the same institution, for their assistance and suggestions. Acknowledgment is also due Dr. A.

[1] Contribution No. 885, Department of Tropical Research, New York Zoological Society.

[2] Hertlein, L. G., and Strong, A. M. Eastern Pacific Expeditions of the New York Zoological Society. XXXII. Mollusks from the West Coast of Mexico and Central America. Part II. *Zoologica*, New York Zool. Soc., Vol. 28, Pt. 3, December 6, 1943, pp. 149-168, pl. 1. See especially pp. 149-150.

Myra Keen, Stanford University, California, for assistance in the identification of some of the species and for the loan of specimens. The preparation of the photographs by Mr. Frank L. Rogers is here acknowledged.

## SUPERFAMILY TELLINACEA.

### FAMILY SANGUINOLARIIDAE.

Key to the genera of the Sanguinolariidae.

A. Shell with posterior gape or chink
 a. Length about four times the height *Tagelus*
 aa. Length about twice the height
  b. Pallial sinus wider anterior to the posterior adductor impression; shell elliptical; periostracum sometimes (subgen. *Nuttalia*) shiny *Sanguinolaria*
  bb. Pallial sinus not wider (or only slightly so) anterior to the posterior adductor impression; shell subrectangular; periostracum dull *Gari*

B. Shell without posterior gape or chink *Heterodonax*

### Genus **Gari** Schumacher.

Key to the subgenera of *Gari.*

A. Shell somewhat pointed posteriorly; compressed; only slightly gaping..... *Gari s.s.*[3]

B. Shell bluntly rounded posteriorly; decidedly gaping ........................*Psammocola*

### Subgenus **Psammocola** Blainville.

Key to the species of *Psammocola.*

A. Posterior area ornamented with fine radial grooves; shell elongate....*regularis*

B. Posterior area ornamented with lines of growth only
 a. Shell subquadrate; posterior end truncately rounded; purplish ..............*lata*[3]
 aa. Shell rectangular; posterior end obliquely truncately rounded; yellowish-white with brownish-pink or purplish rays ........................*maxima*

### **Gari (Psammocola) maxima** Deshayes.

*Psammobia maxima* Deshayes, *Proc. Zool. Soc. London* for 1854, p. 317 (issued May 8, 1855). "Hab. — ? Coll. Cuming." — Reeve, Conch. Icon., Vol. 10, *Psammobia*, 1857, species 4, pl. 1, fig. 4. "Hab. Panama."

*Type Locality*: Panama. [Cited as locality for the species by Reeve and designated as type locality by the present authors]. No locality originally cited.

*Range*: Georges Island, Gulf of California, to Gorgona Island, Colombia.

*Collecting Station*: Colombia: Gorgona Island.

*Description*: Shell ovately rectangular, inequilateral, somewhat compressed, rounded anteriorly, somewhat steeply, obliquely, roundly truncated and gaping posteriorly; ornamented with rude concentric growth striae and ridges; yellowish-white and rayed with brownish-pink or purple; pallial sinus extending nearly to or slightly beyond a line vertical with the beaks, rounded anteriorly and for about one-half its length confluent with the pallial line.

The single specimen in the present collection measures approximately: length, 54 mm.; height, 33 mm.; convexity (both valves together), 16 mm.; pallial sinus extends anteriorly 32 mm. from the posterior end of the shell.

*Gari lata* Deshayes[4] described from Central America and Santa Elena, Ecuador, is less elongate and more quadrate in outline and the posterior end is less obliquely truncated.

*Distribution*: Only one specimen of this species was taken by the expedition at Gorgona Island, Colombia. This record furnishes a slight extension south of the known range of the species.

### **Gari (Psammocola) regularis** Carpenter.

Plate II, Fig. 10.

*Psammobia (?Amphichaena) regularis* Carpenter, *Ann. & Mag. Nat. Hist.*, Ser. 3, Vol. 13, April, 1864, p. 312. From "Cape St. Lucas." Reprint in *Smithson. Miscell. Coll.*, No. 252, 1872, p. 210.

*Psammobia regularis* Carpenter, I. S. Oldroyd, *Stanford Univ. Publ. Univ. Ser. Geol. Sci.*, Vol. 1, 1924, p. 184. San Diego, California, to Cape San Lucas, Lower California.

*Type Locality*: Cape San Lucas, Lower California, Mexico.

*Range*: Catalina Island, California, to the Gulf of California and south to Port Guatulco, Mexico.

*Collecting Stations*: Mexico: Gorda Banks (150-D-6), 60 fathoms, muddy sand, rocks; Point Arena; Port Guatulco (195-D-9), 7 fathoms, gr. sand, crushed shell.

*Description*: Shell elongate, nearly equilateral, anterior end rounded, posterior end roundly truncated, posterior dorsal area depressed and ornamented with fine, radial, incised lines; exteriorly and interiorly mottled with white and purple, the exterior covered with a golden brown periostracum; hinge of right valve with a strong cardinal, the left with a cardinal and a thin posterior lamella; pallial sinus blunt or bluntly rounded at anterior end and extending to or slightly beyond a line vertical with the beaks, and for about half its length confluent with the pallial line.

A specimen from Ceralbo Island, Gulf of California, in the collections of the California Academy of Sciences, measures: length, 46.8 mm.; height, 25 mm.; convexity (both valves together), 15 mm.; pallial sinus extends anteriorly 25 mm. from the posterior margin of the shell.

The shell of this species is very much more elongate than that of *Gari maxima* Deshayes

[3] Not represented in the present collection.

[4] *Psammobia lata* Deshayes, *Proc. Zool. Soc. London* for 1854, p. 318 (issued May 8, 1855). "Hab. Central America; Sancta Elena. Coll. Cuming."—Reeve, Conch. Icon., Vol. 10, *Psammobia*, June, 1857, species 7, pl. 1, fig. 7. "Hab. St. Elena, West Columbia; Cuming."

and the posterior area is ornamented with fine incised lines rather than smooth.

*Distribution*: This species has been recorded previously from southern California to the Gulf of California. The present record from Port Guatulco, Mexico, furnishes an extension south of the known range of this species.

Genus **Sanguinolaria** Lamarck.

Key to the subgenera of *Sanguinolaria*.

A. Pallial sinus entirely confluent below with pallial line ..................... *Sanguinolaria s.s.*
B. Pallial sinus confluent below for about ½ its length with pallial line...... *Psammotella*

Subgenus **Sanguinolaria s.s.**

Key to the species of *Sanguinolaria s.s.*

A. Shell colored entirely red or pink
 a. Shell very thin; about 35 mm. in length *purpurea*
 aa. Shell thick; large, about 50-75 mm. in length .................................. *tellinoides*
B. Shell pink on umbonal area, white or buff below ........................................... *vespertina*

**Sanguinolaria (Sanguinolaria) purpurea** Deshayes.

Plate II, Figs. 5 & 8.

*Sanguinolaria purpurea* Deshayes, *Proc. Zool. Soc. London* for 1854, p. 346 (issued May 16, 1855). "Hab.—? Coll. Cuming."—Reeve, Conch. Icon., Vol. 10, *Sanguinolaria*, 1857, species 5, pl. 1, fig. 5. Hab.—?—Carpenter, Cat. Mazatlan Shells, August, 1855, p. 31, Mazatlan, Mexico.

*Type Locality*: No locality cited originally. Mazatlan, Mexico (here designated as type locality).

*Range*: San Lucas Bay, Lower California, to Mazatlan, Mexico.

*Collecting Station*: Mexico: San Lucas Bay, Lower California (135-D-25), 7 fathoms, sand.

*Description*: S. testa ovato-transversa, tenui, fragili, pellucida, convexiuscula, inaequilaterali, omnino intus extusque purpureo-sanguinea, transversim obsolete et irregulariter striata; latere antico breviore, lato, semielliptico, superne inferneque convexiusculo; latere postico attenuato, superne recto, declivi, obtuso, hiante; cardine in unaquaque valva inaequaliter bidentato; sinu pallii triangulari, superne angulato, antice oblique truncato, impressionem muscularem posticam versus longe strangulato. (Original description).

Shell ovately transverse, thin, fragile, transparent, flatly convex, inequilateral, transversely closely striated, interior deep shining blood-purple, anterior side rounded, posterior regularly attenuately rounded. (Reeve).

The specimen of this species in the present collection measures approximately: length, 34 mm.; height, 21 mm.; convexity (both valves together), 9 mm.; pallial sinus extends anteriorly 26.5 mm. from the posterior margin of the shell.

The pallial sinus in the present specimen is confluent below with the pallial line. This feature does not agree with Reeve's illustration where the pallial sinus is free from the pallial line. We are uncertain as to whether or not this feature as shown in Reeve's figure can be regarded as characteristic of this species because in similar species the sinus is usually entirely or at least partly confluent with the pallial line.

Carpenter's remarks (1855) on *Sanguinolaris purpurea* agree well with our specimen but it is also true that later[5] he referred that record to *S. miniata* Gould, a species now believed to be identical with *S. tellinoides* A. Adams.

The present specimen differs from *S. tellinoides* in that it is thinner, more oval in outline, less pointed posteriorly, the pallial sinus is somewhat more abruptly truncated anteriorly and the color is more of a deep "blood-purple" as mentioned by Deshayes and Reeve. The thinner shell, the color which covers the entire shell and the less expanded anterior dorsal margin are characters which serve to separate this species from *S. vespertina* Pilsbry & Lowe.

*Distribution*: A single specimen of this species was dredged by the expedition in San Lucas Bay in 7 fathoms. At the present time this rare species is known to occur only in the southern portion of the Gulf of California region, at Mazatlan and San Lucas Bay.

**Sanguinolaria (Sanguinolaria) tellinoides** A. Adams.

*Sanguinolaria tellinoides* A. Adams, *Proc. Zool. Soc. London* for 1849, p. 170, pl. 6, fig. 6, (issued January to June, 1850). "Hab. in Sinu Californiae." — Reeve, Conch. Icon., Vol. 10, *Sanguinolaria*, 1857, species 3, pl. 1, fig. 3. "Hab. Gulf of California."

*Tellina miniata* Gould, *Proc. Boston Soc. Nat. Hist.*, Vol. 4, November, 1851, p. 90. "Inhabits San Juan." [Lower California].—Gould, *Boston Jour. Nat. Hist.*, Vol. 6, October, 1853, p. 397, pl. 16, fig. 1. "Inhabits San Juan."

*Type Locality*: Gulf of California.

*Range*: Gulf of California to Gorgona Island, Colombia.

*Collecting Stations*: Nicaragua: Potosi and Monypenny Point, Gulf of Fonseca, beach; Costa Rica: Gulf of Dulce, beach; Colombia: Gorgona Island, beach.

*Description*: Shell elongately oval, inequilateral, anterior side the shorter, broader and rounded; posterior side somewhat feebly flexuously impressed from the umbos, attenuated and roundly pointed at the end; fresh specimens are minutely decussately striated; color deep rose, sometimes purplish-red around the beak and umbonal area; pallial sinus fairly high and angulated in the middle, confluent with the pallial line below.

[5] Carpenter, P. P., *Proc. Zool. Soc. London* for 1856, p. 199 (issued January 7, 1857).

The largest specimen in the present collection, slightly worn, measures approximately: length, 75 mm.; height, 44 mm.; convexity (one valve), 10.5 mm.; pallial sinus extends anteriorly 61 mm. from the posterior margin of the shell.

An elongate variety of *S. tellinoides* was named *elongata* by Mörch.[6]

Compared to *Sanguinolaria bertini* Pilsbry & Lowe, the shell of *S. tellinoides* is higher in proportion to the length, much wider posteriorly, and the pallial sinus is high and angulated rather than rounded.

*Sanguinolaria sanguinolenta* Gmelin is a somewhat similar species in east American waters.

*Distribution*: The present record of the occurrence of *Sanguinolaria tellinoides* at Gorgona Island, Colombia, is a slight extension southward of the known range of the species.

### Sanguinolaria (Sanguinolaria) vespertina Pilsbry & Lowe.

*Sanguinolaria vespertina* Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 84, May 21, 1932, p. 90, pl. 12, figs. 3 and 4 (as *Semele vespertina* on expl. to pl.). Type from "San Juan del Sur, Nicaragua (Lowe)." Also, Corinto, Nicaragua.

*Type Locality*: San Juan del Sur, Nicaragua.

*Range*: Tangola-Tangola Bay, Oaxaca, Mexico, to Uvita Bay, Costa Rica.

*Collecting Stations*: Mexico: Tangola-Tangola Bay, beach; Costa Rica: Uvita Bay, beach.

*Description*: Shell with the general characters of *Sanguinolaria tellinoides* but smaller, more ovate, more inflated, the anterior dorsal area more expanded, the posterior end wider; ornamented with concentric lines of growth and some very weak radiating striae; colored deep pink on the beaks and umbonal region but whitish or buff on the lower half. Generally 25 to 30 mm. in length.

The shell of this species is similar to that of the east American *Sanguinolaria sanguinolenta* Gmelin but is thinner, the hinge plate is narrower and the teeth are smaller.

*Sanguinolaria ovalis* Reeve[7] was described from Central America. According to the description it is thin-shelled, especially convex in the umbonal region and whitish tinged with pink. The illustration indicates that the anterior dorsal margin is somewhat expanded similar to that of *S. vespertina*. Mörch[8] considered *S. ovalis* to be a valid species but Dall[9] considered it to be a young form of *S. tellinoides*. From the illustration it is difficult to determine with certainty whether or not it might be identical with *S. vespertina* and accordingly we have retained the name proposed by Pilsbry & Lowe which undoubtedly applies to the present specimens.

*Distribution*: Two small specimens referred to *Sanguinolaria vespertina* in the present collection furnish an extension both to the north and to the south of the known range of this species.

Subgenus **Psammotella** Herrmannsen.

*Psammotelle* Blainville, Dict. Sci. Nat., Vol. 52, 1826, p. 541. [Vernacular].

*Psammotella* Herrmannsen, *Indic. Gen. Malacol.*, Suppl., December, 1852, p. 114. Sole species: "*T. rufescens* Chemn." — Dall, *Trans. Wagner Free Inst. Sci.*, Vol. 3, Pt. 5, 1900, p. 978. Type: *P. operculata* Gmelin (= *Tellina rufescens* Chemnitz).

*Type* (by monotypy): *Tellina rufescens* Chemnitz, Neues Syst. Conchyl.-Cab., Bd. 6, 1782, p. 105, Taf. 11, fig. 97 [which= *Tellina operculata* Gmelin, Syst. Nat., ed. 13, Tom. 1, Pars 6, 1790, p. 3235. "Habitat in India? rarior." Reference to Chemnitz, Bd. 6, pl. 11, fig.97, and Knorr, Vergn., Vol. 6, pl. 12, fig. 1?]. [West Indies].

Shell elongate, rostrate, inequivalve, the left valve flattened; pallial sinus discrepant in the two valves, narrower in front, partly confluent with the pallial line, otherwise like *Sanguinolaria*. (Dall).

### Sanguinolaria (Psammotella) bertini Pilsbry & Lowe.

*Tellina rufescens* Chemnitz, Hanley, Thes. Conch., Vol. 1, 1846, p. 307 pl. 63, fig. 213. "Tumbez, Peru; soft sandy mud, five fathoms (Cuming)."

Not *Tellina rufescens* Chemnitz, Neues Syst. Conchyl.-Cab., Bd. 6, 1782, p. 105, Taf. 11, fig. 97.

Not *Tellina rufescens* Gmelin, Syst. Nat., ed. 13, Tom. 1, Pars 6, 1790, p. 3238. "Habitat—." Ref. to Gualtieri, Test., Tab. 85, fig. C.

Not *Tellina rufescens* Dillwyn, Descript. Cat. Rec. Shells, Vol. 1, 1817, p. 85. "Inhabits the coast of Brazil. Humphreys."

*Tellina hanleyi* Bertin, *Nouv. Arch. Mus. Hist. Nat.* (Paris), Ser. 2, Vol. 1, 1878, p. 268. "Habite les côtes du Pérou et celles de l'Amérique centrale." New name for *Tellina rufescens* Chemnitz cited by Hanley, 1846. Not *T. rufescens* Chemnitz, 1782. Brazil.

Not *Tellina hanleyi* Dunker, 1853.

*Sanguinolaria bertini* Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 84, May 21, 1932, p. 91, pl. 10, figs. 7, 8. Type from Acapulco, Mexico. Also collected at "Panamá (McNeil); Champerico, Guatemala (J. L. Bailey); Montijo Bay, San Juan del Sur, Corinto and Acapulco (Lowe)." A new name for *Tellina rufescens* of Hanley, 1846, not *T. rufescens* Gmelin, 1790, nor Dillwyn, 1817. *Tellina hanleyi* Bertin, 1878, not *T. hanleyi* Dunker, 1853.

*Type Locality*: Acapulco, Mexico.

*Range*: San Ignacio Lagoon, Lower California, to the Gulf of California and south to Lobitos, Peru.

---

[6] [*Sanguinolaria tellinoides*] var. *elongata* Mörch, *Malakozool. Blätter*, Bd. 7, December, 1860, p. 185.

[7] *Sanguinolaria ovalis* Reeve, Conch. Icon., Vol. 10, *Sanguinolaria*, March, 1857, species 2, pl. 1, fig. 2. "Hab. Central America."

[8] Mörch, O. A. L., *Malakozool. Blätter*, Bd. 7, December, 1860, p. 185. Sonsonate, El Salvador.

[9] Dall, W. H., *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 50, 1898, p. 61.

*Collecting Station*: Costa Rica: Gulf of Dulce.

*Description*: Shell rather narrowly elongate, gaping, left valve flattened, anterior end elliptically rounded, the posterior end rostrate and bluntly pointed; posterior dorsal margin depressed, and a depressed radial area occurs anterior to the rounded umbonal ridge; often with sub-obsolete radial striae; color dark rose in zones and darker toward the beaks; pallial sinus rounded, extending about two-thirds the length of the shell and for about two-thirds its length confluent with the pallial line.

A specimen collected in the Gulf of Dulce, Costa Rica, measures: length, 57 mm.; height, 28.6 mm.; convexity (both valves together), 12.5 mm.; pallial sinus extends anteriorly 38.8 mm. from the posterior margin of the shell. A large right valve collected on the coast below San Ignacio Lagoon, Lower California, in the Henry Hemphill collection of the California Academy of Sciences, measures: length, 91.8 mm.; height, 47 mm.; convexity (one valve), 14 mm.; pallial sinus extends anteriorly 65 mm. from the posterior margin of the shell.

There is an element of doubt regarding the correct name of this species. Hanley (1846) cited *Tellina rufescens* Chemnitz from Peru but the true *T. rufescens* Chemnitz is from Brazil as indicated by Dillwyn. Bertin in 1878 named the west American form *Tellina hanleyi*. Pilsbry & Lowe pointed out that there is a prior usage of that combination of names, that of *Tellina hanleyi* Dunker, 1853, from Loanda, West Africa. They therefore renamed the west American species *Sanguinolaria bertini*, based on a type specimen from Acapulco, Mexico.

Salisbury[10] in 1934 stated that the west American species named *Tellina hanleyi* by Bertin and later renamed by Pilsbry & Lowe can take the name of *Tellina cruentae* Solander.[11] The name *Tellina cruentae* was used by Solander in the Catalogue of the Portland Museum on page 10 and as *Tellina cruenta* on page 58 where a reference was given citing "Knorr. VI. 12.1." Gmelin cited this figure of Knorr as representing his *Tellina operculata*. Dillwyn, who had access to the Banks Collection and Solander's manuscript of the Portland Catalogue, likewise cited Knorr's reference under the east American "*Tellina*" *operculata* Gmelin. Pilsbry,[12] in discussing the conclusion of Salisbury, stated that it seems unlikely that Knorr would have had the west American shell but he also admitted that "While it seems rather unlikely that this west American shell was possessed by Knorr prior to 1771, it is possible, and his figure is certainly very good for it." He recommended the spelling *cruenta*, used by Solander on page 58, if the name is to be adopted.

[10] Salisbury, A. E., *Proc. Malacol. Soc. London*, Vol. 21, Pt. 2, 1934, p. 88.

[11] *Tellina cruentae* Solander, Cat. Portland Mus., 1786, p. 10, "*cruenta*" on p. 58. See also Dall, W. H., *Nautilus*, Vol. 34, No. 3, 1921, p. 99.

[12] Pilsbry, H. A., *Nautilus*, Vol. 49, No. 4, 1936, p. 140.

We have not seen Knorr's figure but in view of the foregoing opinions expressed by various authors we are inclined to use the specific name *bertini* until it is more definitely proved that Solander's name *cruenta* can be applied to it.

The shell of *Sanguinolaria bertini* is very similar to the east American *S. operculata* Gmelin but in general it is narrower posteriorly and the pallial sinus is usually a little more arched posteriorly and confluent with the pallial line for a greater distance than that of the east American species.

*Distribution:* This species was taken only in the Gulf of Dulce but it occurs from Lower California to Peru.

### Genus **Heterodonax** Mörch.

### **Heterodonax bimaculata** Linnaeus.

*Tellina bimaculata* Linnaeus, Syst. Nat., ed. 10, 1758, p. 677. "Habitat in O. Europaeo." — Chemnitz, Neues Syst. Conchyl.-Cab., Bd. 6, 1782, p. 132, pl. 13, fig. 127, fig. 132 lit. a, b. "Sie wohnet an den westindischen Ufern, und an einigen Stranden der europaischen Meere." — Sowerby, Conch. Icon., Vol. 17, *Tellina*, 1866, species 94, pl. 18, figs. 94a, 94b, 94c. West Indies.

*Psammobia pacifica* Conrad, *Jour. Acad. Nat. Sci. Philadelphia*, Vol. 7, 1837, p. 241, pl. 18, fig. 13. "Inhabits in deepish water on a sandy bottom, near Sta. Diego." California.

*Tellina vicina* C. B. Adams, *Ann. Lyceum Nat. Hist. New York*, Vol. 5, July, 1852, pp. 509, 546 (separate pp. 285, 322). "Panama."

*Donax ovalina* Deshayes, *Proc. Zool. Soc. London* for 1854, p. 352 (issued May 16, 1855). "Hab. Central America. Coll. Cuming." — Sowerby, Thes. Conch., Vol. 3, 1866, p. 312, pl. 283 (*Donax*, pl. 4), fig. 104 (as *Donax ovalinus*).

*Type Locality*: Europe originally cited. West Indies cited as type locality by I. S. Oldroyd, 1924.

*Range*: Monterey, California, to Panama. Also Florida to Brazil.

*Collecting Stations*: Mexico: Cape San Lucas, beach; Port Guatulco, beach; Nicaragua: Potosi and Monypenny Point, beach; Costa Rica: Port Parker, beach; Port Culebra and Culebra Bay, beach; Golfito, beach.

*Description*: Shell triangularly rounded, inequilateral, the anterior side the longer, the posterior end rounded or roundly truncated, smooth, variously colored, white with two oblong crimson spots on the inside, or violet with oblong radial reddish streaks, or pink, orange, or some combination of the foregoing; two cardinals and two laterals in each valve, the laterals often not well defined; pallial sinus extends about three-fifths the length of the shell, slightly ascending, the end blunt, obliquely rounded below, confluent below with the pallial line for only a short distance or sometimes for a third its length.

A large specimen collected at San Diego, California, by Henry Hemphill measures: length, 27.3 mm.; height, 22.5 mm.; convexity (both valves together), 11 mm.; pallial

sinus extends anteriorly 15.6 mm. from the posterior margin of the shell.

This species has received a number of different names due probably to the variation in form and color as well as the wide distribution. Specimens from both the Atlantic and Pacific coasts are referable to the species described by Linnaeus as *Tellina bimaculata*.

*Heterodonax alexandra* Dall,[13] described from the Pliocene of Louisiana, was compared to *H. bimaculata*.

*Distribution*: Specimens of *Heterodonax bimaculata* were taken by the expedition along the beach from Mexico to Costa Rica. It is often found near the high tide line on sandy shores of bays in southern California. This is one of the species common to the Atlantic and Pacific coasts of America. Forbes and Hanley[14] pointed out that early records of *H. bimaculata* (as *Tellina bimaculata*) from the coasts of Great Britain were probably based on specimens spuriously introduced there. It has also been reported as occurring in the Pleistocene of southern California and at Magdalena Bay, Lower California, as well as in the Caribbean region.

### Genus **Tagelus** Gray.

Key to the subgenera of *Tagelus*.

A. Shell with internal radial rib (sometimes faint or lacking in adult) ........*Mesopleura*

B. Shell without internal rib........*Tagelus s.s.*

### Subgenus **Tagelus s.s.**

Key to the species of *Tagelus s.s.*

A. Pallial sinus not extending past a line vertical with the beaks................*californianus*

B. Pallial sinus extending past a line vertical with the beaks

  a. Shell large (length often exceeding 60 mm.), thick; violet coloration externally on umbonal areas..........*violascens*

  aa. Shell smaller (length usually less than 60 mm.), thin; white or brownish

    b. Shell rather short; pallial sinus extends anteriorly about 53% the length of the shell..................*affinis*

    bb. Shell more elongate; pallial sinus extends anteriorly about 60% the length of the shell *longisinuatus*[15]

### **Tagelus (Tagelus) affinis** C. B. Adams.

Plate I, Figs. 9 & 11.

*Solecurtus affinis* C. B. Adams, *Ann. Lyceum Nat. Hist. New York*, Vol. 5, July, 1852, pp. 524, 548 (separate pp. 300, 324). "Panama."

*Silicaria affinis* C. B. Adams, Mörch, *Malakozool. Blätter*, Bd. 7, December, 1860, p. 184. Realejo, Nicaragua.

*Type Locality*: Panama.

*Range*: Gulf of California to Panama.

*Collecting Stations*: Mexico: Chamela Bay, beach; El Salvador: Meanguera Island, Gulf of Fonseca (199-D-1), 16 fathoms, sand, mud, crushed shell; La Union, Gulf of Fonseca (199-D-8, 13-16, 22-25), 3-6 fathoms, mud, mangrove leaves; Costa Rica: Port Parker, beach; Port Culebra, beach; Culebra Bay, beach; Panama: Gulf of Chiriqui (221-D-1-5), 35-40 fathoms, sandy mud.

*Description*: Shell much elongated, compressed, cylindric, well rounded at both extremities; ventral edge straight or slightly arcuated: white beneath a deep yellowish brown epidermis: with unequal striae of growth: beaks not prominent, a little behind the middle of the shell: umbones compressed along the middle: ligament broad, with stout nymphaeal callosities: teeth small, one in the left, and two in the right valve. This is the analogue of *S. cariboeus*. Length, 2.25 inches; height, .8 inch; breadth, .55 inch. (Original description).

A specimen in the collections of the California Academy of Sciences collected in Panama Bay by F. M. Anderson measures: length, 56.4 mm.; height, 20.8 mm.; convexity (both valves together), 14 mm.; pallial sinus extends anteriorly 30.4 mm. from the posterior end of the shell.

The pallial sinus in typical *Tagelus affinis* extends to a line slightly beyond the beaks, that is, about 53 per cent. of the length of the shell. The anterior end of the sinus is broadly rounded and joins the pallial line with only a slight bend posteriorly. The length of the shell and of the pallial sinus varies somewhat. The shells in the northern part of the range are often narrower and more elongate with a narrower and more acutely rounded pallial sinus which extends about 60 per cent. of the length of the shell, that is, well past a line vertical with the beaks. This form is known as *Tagelus affinis longisinuatus* Pilsbry & Lowe.[16]

*Tagelus peruanus* Dunker,[17] described from Peru, is very similar to *T. affinis*. According to Sowerby's illustration the shell is a little higher in proportion to the length as compared to Adams' species.

*Distribution*: This species was taken from Chamela Bay, Mexico, to the Gulf of Chiriqui, Panama, on beaches and dredged at depths of 3-40 fathoms.

### **Tagelus (Tagelus) californianus** Conrad.

Plate I, Fig. 1.

*S[olecurtus]. californianus* Conrad, *Jour. Acad. Nat. Sci. Philadelphia*, Vol. 7, 1837, p. 233, pl. 18, fig. 3. "Inhabits muddy salt marshes, in the neighborhood of Sta. Bar-

---

[13] *Heterodonax alexandra* Dall, *Proc. U. S. Nat. Mus.*, Vol. 46, December 6, 1913, p. 228, pl. 20, fig. 8. From "near Alexandria, Louisiana." Pliocene.

[14] Forbes, E., and Hanley, S., Hist. Brit. Moll., Vol. 1, 1853 (issued 1848), pp. 310-311. For dates of issue of this work see Tomlin, J. R. le B., and Fisher, N., *Jour. Conch.*, Vol. 20, No. 5, August 22, 1935, pp. 150-151.

[15] Not represented in the present collection.

[16] *Tagelus affinis longisinuatus* Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 84, May 21, 1932, p. 91, pl. 11, figs. 4 and 5. "Mazatlan."

[17] *Siliquaria peruana* Dunker, *Proc. Zool. Soc. London*, December 10, 1861, p. 426. "Hab. in littore Peruano (H. Cuming)."

*Solecurtus peruanus* Dunker, Sowerby, Conch. Icon., Vol. 19, *Solecurtus*, November, 1874, species 38, pl. 8, fig. 38. "Hab. Tumbez, Peru."

bara; Common." — Sowerby, Conch. Icon., Vol. 19, *Solecurtus*, 1874, species 36, pl. 8, fig. 36. "Hab. California."

*Tagelus californianus* Conrad, Grant & Gale, *Mem. San Diego Soc. Nat. Hist.*, Vol. 1, 1931, p. 384, pl. 21, figs. 2a, 2b, 3. Earlier records cited, Pliocene to Recent.

*Type Locality*: Neighborhood of Santa Barbara, California, muddy salt marshes.

*Range*: Monterey, California, to the Gulf of California and south to Panama.

*Collecting Stations*: Mexico: Cape San Lucas, Lower California, beach; Costa Rica: Port Culebra, beach.

*Description*: Shell elongated, compressed, beaks nearly central, dorsal and ventral margins nearly parallel, anterior end broadly rounded, posteriorly with a rounded umbonal ridge and with the posterior area somewhat flattened and in young forms the periostracum on this portion is often radially striated, the end truncated; color exteriorly yellowish-white under a dark brown periostracum, interior white; the pallial sinus varies somewhat but usually does not extend to a line vertical with the beaks, it is rather acutely rounded anteriorly and at the junction with the pallial line forms an acute angle.

A large specimen collected at San Diego, California, by Henry Hemphill, measures approximately: length, 112 mm.; height, 31.5 mm.; convexity (both valves together), 20 mm.; pallial sinus extends anteriorly 50 mm. from the posterior end of the shell. Orcutt mentioned specimens from Santo Domingo, Lower California, which measured 120 mm. in length.

Compared to *Tagelus affinis* the shell of *Tagelus californianus* is much longer in proportion to the height, thicker, the flattened posterior area is more pronounced and, in young forms, the periostracum is radially striated, the pallial sinus is usually shorter, more acutely rounded, and at the junction with the pallial line, which takes place proportionately farther anteriorly, it forms an acute angle. Compared to *T. violascens*, the anterior dorsal margin of *T. californianus* is usually somewhat straighter, the pallial sinus is shorter and the shell is yellowish-white exteriorly rather than violet on the umbonal region.

*Distribution*: One valve of this species was taken on the beach at Cape San Lucas, Lower California, and one single valve was taken on the beach at Port Culebra, Costa Rica. It is also known to occur from Pliocene to Recent in western North America.

**Tagelus (Tagelus) violascens** Carpenter.

Plate I, Figs. 4 & 6.

*Solecurtus violascens* Carpenter, Cat. Mazatlan Shells, August, 1855, p. 27 (footnote). "Hab. S. W. Mexico." — Sowerby, Conch. Icon., Vol. 19, *Solecurtus*, 1874, species 24, pl. 58, fig. 24. "Hab. S. W. Mexico."

*Type Locality*: Southwest Mexico.

*Range*: Gulf of California to Port Culebra, Costa Rica.

*Collecting Station*: Costa Rica: Port Culebra.

*Description*: "S. t. 'S. affine' simili, sed majore, solida, violascente, rugis epidermidis tenuioribus; nymphis elongatis, sinu pallii versus umbones minus arcuato. Long. .95, lat. 3.33, alt. .56." (Original description).

Carpenter compared this species with *Tagelus politus* and *T. affinis* and stated that with regard to color it is intermediate between these two. He also mentioned that the anterior adductor impression of *T. violascens* tapers off irregularly, uniting with the two small impressions which occur between the umbo and the anterior impression.

One right valve in the collection from Port Culebra, Costa Rica, measures: length, 83 mm.; height, 26 mm.; convexity (one valve), 8 mm.; the pallial sinus extends anteriorly 39 mm. from the posterior end (incomplete) of the shell. It is somewhat worn and shows only traces of the violet coloration on the umbonal region. A specimen in the collection of Stanford University, which was collected by H. N. Lowe at Salina Cruz, Oaxaca, Mexico, measures: length, 85 mm.; height, 30 mm.; convexity (both valves together), 21.8 mm.; pallial sinus extends anteriorly 47 mm. from the posterior end of the shell.

As mentioned by Carpenter the shell of this species is larger, more elongate and thicker than that of *Tagelus affinis*. It bears considerable similarity to *T. californianus* but differs from that species in the violet coloration, greater height in proportion to the length, usually more arcuate anterior dorsal margin and in that the pallial sinus is longer and extends past a line vertical with the beaks.

*Distribution*: The present record of *Tagelus violascens* from Port Culebra, Costa Rica. is an extension south of the known occurrence of this species. Some of the records in the literature referring to this species are referable to *Tagelus politus*. Olsson has reported *T. violascens* as occurring in the Pleistocene of Panama.

Subgenus **Mesopleura** Conrad.

Key to the species of *Mesopleura*.

A. Posterior dorsal margin with a flange-like expansion ........ *peruvianus*

B. Posterior dorsal margin without a flange-like expansion

  a. Shell thin and narrow

    b. Dorsal margins slope very gently from the beaks; dark violet coloration ........ *politus*

    bb. Dorsal margins slope more steeply from the beaks; light violet coloration ........ *subteres*

  aa. Shell thick and comparatively higher and larger ........ *dombeii*[18]

[18] Not represented in the present collection.

### *Tagelus (Mesopleura) peruvianus* Pilsbry & Olsson.

*Tagelus (Mesopleura) peruvianus* Pilsbry & Olsson, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 93, September 9, 1941, p. 70, pl. 18, fig. 5. "Punta Blanca beds." Ecuador, Pliocene. Also Recent, coast of northwest Peru and Ecuador.

*Type Locality*: Punta Blanca beds of Ecuador, Pliocene.

*Range*: Port Culebra, Costa Rica, to Negritos, Peru.

*Collecting Station*: Costa Rica: Port Culebra, beach.

*Description*: The shell is broad, elongate, its height about a third of its length, parallel sided, and of moderate convexity; the small beak is located not quite centrally, the posterior end being the longer; ventral margin straight, the dorsal a little arched on the anterior side, winged on the posterior; ends rounded, the posterior obliquely so; surface marked by growth-lines which are strongest on the anterior and posterior ends; the shells are usually a little warped in the middle, producing a small gap at each end; when young the interior shows the well-marked thickened ray of *Mesopleura*, but in the adult this rib may disappear entirely or persists only in a slight thickening of this part of the shell; pallial sinus ample, rounded, higher within the shell than at its opening, reaching not quite to the middle of the length. When young the shell is quite thin, translucent, tinged with lilac, the rays brownish; epidermis dark olive-black usually absent from the umbones, which are light-colored and rayed. Length, 85 mm.; height, 28.5 mm.; semidiameter, 8 mm. (Original description).

The type of this species is a fossil but the last sentence in the description was based on Recent shells.

The shell of this species differs from *Tagelus (Mesopleura) dombeii* Lamarck,[19] which also was described from South America, in that the shell is proportionately higher and is characterized by a flange or wing-like extension of the posterior dorsal margin.

One right valve of this species is represented in the present collection from Port Culebra, Costa Rica. It measures 66.5 mm. in length and 24 mm. in altitude; convexity (one valve), 6.5. mm.; pallial sinus extends anteriorly 29 mm. from the posterior end of the shell. A faint trace of a median rib is present on the interior of the shell. Exteriorly there are two grooves running posteriorly from the beak to the posterior margin, one reaches the margin just below the middle of the posterior end and the other halfway between this and the dorsal margin. It is tinged with purple and brown rays.

*Distribution*: The present record of this species from Port Culebra, Costa Rica, is an extension north of the known range. A left valve of this species 39.5 mm. in length, in the collection of the California Academy of Sciences, was collected by Woodbridge Williams in Santa Elena Bay, Ecuador. This species also is known to occur in the Pliocene of Ecuador and in the Pleistocene of Panama.

### *Tagelus (Mesopleura) politus* Carpenter.

Plate I, Figs. 8 & 10.

*Solecurtus politus* Carpenter, Cat. Mazatlan Shells, August, 1855, p. 27. "Hab.—Mazatlan: 4 specimens found with *affinis*; L'pool Col."

*Type Locality*: Mazatlan, Mexico.

*Range*: Gulf of California to Panama.

*Collecting Stations*: Mexico: Santa Inez Bay, Gulf of California (145-D-1, 3), 4-13 fathoms, sand, also on shore; Port Guatulco (195-D-19, 20, 21), 17-23 fathoms, gr. mud, crushed shell, mud; Tangola-Tangola Bay (196-D-13, 14, 18), 5-30 fathoms, gr. sand, crushed shell, mud; Guatemala: 7 miles west of Champerico (197-D-2), 14 fathoms, mud; El Salvador: La Libertad (198-D-1, 2), 13-14 fathoms, mud; Meanguera Island, Gulf of Fonseca (199-D-1), 16 fathoms, sand, mud, crushed shell; Nicaragua: Corinto, beach; Costa Rica: Port Parker (203-D-1-3), 12-15 fathoms, sandy mud, crushed shell, shelly sand, algae, shelly mud; Cedro Island (213-D-1-10), 4-10 fathoms, mud, sand, crushed shell; 1 mile south of Golfito Bay, shore.

*Description*: Shell thin, subtranslucent, rayed with violet. Carpenter mentioned that it may be "Known at once by the brownish violet colour, glossy epidermis, and dark ray corresponding with a slightly prominent ridge within . . . In the pallial sinus, *S. affinis* is intermediate between *politus and violascens*."

The pallial sinus is rounded anteriorly and extends to the internal median ray.

A valve from Tangola-Tangola Bay, Mexico, measures: length, 35 mm.; height, 12.8 mm.; convexity (one valve), 3.7 mm.; pallial sinus extends anteriorly 16 mm. from the posterior end of the shell. Large specimens attain a length of about 40 mm. or slightly more.

Compared to *Tagelus subteres* Conrad which occurs from Santa Barbara, California, to Cape San Lucas, Lower California, the shell of *T. politus* is usually smaller and thinner, much more darkly colored with violet both exteriorly and interiorly and the dorsal margins slope more gently from the beaks.

*Distribution*: This species was taken at a number of localities from Santa Inez Bay in the Gulf of California to Golfito Bay, Costa Rica, on the beach and also dredged at depths

[19] *Solen dombeii* Lamarck, Anim. s. Vert., Vol. 5, July, 1818, p. 454. "Habite les mers de l'Amérique méridionale, les cotes du Pérou." Reference to Encycl. Meth., pl. 224, figs. 1a, 1b, 1c.—Chenu, Illustr. Conchyl., *Solen*, 1843, pl. 5, figs. 1, 1a, 2, 2a, 2b, 3, 3a, 4, 4a, 5.

*Solecurtus dombei* Lamarck, Sowerby, Conch. Icon., Vol. 19, *Solecurtus*, August, 1874, species 30, pl. 7, figs. 30a, 30b. "Hab. S. America."

*Solecurtus rufa* "Bosch.", Sowerby, Conch. Icon., Vol. 19, *Solecurtus*, August 1874, species 30, pl. 6, fig. 27. "Hab. ———?" Not *Glycimeris rufa* Bosc, Hist. Nat. Coq., Vol. 3, AN X [1801], p. 6, pl. 17, fig. 3. "Se trouve dans les grands fleuves, et lacs de l'Amérique méridionale."

*Solecurtus coquimbensis* Sowerby, Conch. Icon., Vol. 19, *Solecurtus*, August, 1874, species 22, pl. 5, figs. 22a, 22b. "Hab. Coquimbo."

of 4-30 fathoms, usually on a muddy or sandy, shelly bottom. It is a common species along the west Mexican coast and is also known to occur in the Pleistocene of Magdalena Bay, Lower California.

### **Tagelus (Mesopleura) subteres** Conrad.

Plate I, Figs. 12 & 13.

*S[olecurtus]. subteres* Conrad, *Jour. Acad. Nat. Sci. Philadelphia*, Vol. 7, 1837, p. 233, pl. 17, fig. 10. "Inhabits in the vicinity of Sta. Barbara." [California].

*Tagelus subteres* Conrad, Johnson & Snook, Seashore Anim. Pac. Coast (Macmillan Co., New York), 1927 (also ed. 1935), p. 457, fig. 459.

*Type Locality*: Vicinity of Santa Barbara, California.

*Range*: Santa Barbara, California, to Cape San Lucas, Lower California.

*Collecting Station*: Mexico: Cape San Lucas, Lower California, on beach.

*Description*: Shell linear-oval, inflated or subcylindrical, slightly arcuate; beaks central, very obtuse, extremities equally rounded; colour pale purple, obscurely rayed; epidermis yellowish brown, finely wrinkled; teeth two in each valve; posterior tooth of the right valve dilated. Length, two and a quarter inches. (Original description).

A left valve from Cape San Lucas, Lower California, measures: length, 46.8 mm.; height, 15.5 mm.; convexity (one valve), 5 mm. A specimen from San Diego, California, in the Henry Hemphill Collection in the California Academy of Sciences, measures: length, 45.6 mm.; height, 14.5 mm.; convexity (both valves together), 9 mm.

A left valve of a *Tagelus* from Cape San Lucas, Lower California, in the present collection appears to be referable to *Tagelus subteres* Conrad. The size of this specimen (46.8 mm. in length) and the comparatively thick shell as well as the slope of the dorsal margins agree well with Conrad's species.

Compared to *Tagelus politus* Carpenter, the shell of *T. subteres* is usually larger, thicker, the dorsal margins slope more strongly from the beaks and the violet coloration is much paler both exteriorly and interiorly.

*Distribution*: A single left valve of this species was collected by the expedition on the beach at Cape San Lucas, Lower California. It also has been recorded as occurring in the Pleistocene at San Quintin Bay, Lower California.

## SUPERFAMILY SOLENACEA.

### FAMILY SOLENIDAE.

Key to the genera and subgenera of the Solenidae.

A. Shell with oblique clapboard sculpture exteriorly .................................... *Solecurtus*
B. Shell smooth
  a. Beaks terminal
    b. One cardinal tooth in left valve ... *Solen*
    bb. Two cardinal teeth in left valve ... *Ensis*
  aa. Beaks not terminal ... (subgenus) *Solena*[20]

### Genus **Solen** Linnaeus.

Key to the species of *Solen*.

A. Shell colored with purple or rose
  a. Shell very elongate; pale rose color on umbos .................................. *rosaceus*
  aa. Shell higher in proportion to the length; purple banded
    b. Periostracum with triangle of darker color on each valve *pazensis*
    bb. Periostracum with even brown color over entire valves....*pfeifferi*
B. Shell white
  a. Elongate; length (type), 60 mm., height, 8.5 mm. ............. *mexicanus*[21]
  aa. Higher in proportion to the length; length (type), 38.8 mm., height, 10.5 mm. .................................... *crockeri*

### **Solen crockeri** Hertlein & Strong, sp. nov.

Plate I, Figs. 3, 5 & 7.

Shell small, short, thin, white, nearly straight, parallel-sided, convex, beaks at anterior end; anterior end steeply obliquely truncated; posterior end nearly squarely truncated but sloping slightly anteriorly; hinge and ligament normal; shell covered with a thin, light olive translucent periostracum. Length, 38.8 mm.; length of ligament, 6 mm.; height, 10.5 mm.; convexity (both valves together), 6.8 mm.

Holotype, (Calif. Acad. Sci. Paleo. Type Coll.), from Station 199-D-3, Lat. 13° 03′ N., Long. 87° 30′ W., Monypenny Point, Nicaragua, in the Gulf of Fonseca, dredged in 6 fathoms (11 meters), mud. Paratypes and additional specimens in the immediate vicinity (Sta. 199-D-1, 5, 8, 14, 16), 5-16 fathoms, sand, mud, crushed shell, mangrove leaves.

This new species appears to be similar to *Solen mexicanus* Dall but is very much higher in proportion to the length. *Solen mexicanus* Dall,[22] a white shell with an unusually long ligament, was described from the Gulf of Tehuantepec, Mexico, and was compared to *Solen linearis* Chemnitz. The type has not been illustrated but the measurements given were: "Length of shell, 60 mm.; of ligament, 11 mm.; width of valves, 8.5 mm.; diameter, 5.5 mm."

The white shell and greater height in proportion to the length are features which serve to separate *Solen crockeri* from *Solen pfeifferi* Dunker and *S. pazensis* Lowe.

This species is named for Mr. Templeton Crocker, enthusiastic collector, whose yacht

[20] Not represented in the present collection. *Solen rudis* C. B. Adams, described from Panama, is referable to this subgenus.

[21] Not represented in the present collection.

[22] *Solen mexicanus* Dall, *Proc. U. S. Nat. Mus.*, Vol. 22, No. 1185, October 9, 1899, p. 110. "Specimen from the Gulf of Tehuantepec." Also recorded as occurring at Digg's Point, Gulf of California (see Eyerdam, *Min. Conch. Club South. Calif.*, No. 47, April, 1945, p. 28).

*Zaca* was used on the expedition during which the type specimens were collected.

### **Solen pazensis** Lowe.

*Solen pazensis* Lowe, *Trans. San Diego Soc. Nat. Hist.*, Vol. 8, No. 6, March 21, 1935, p. 17, pl. 1, fig. 6. "La Paz, Lower California, tidal zone."

*Type Locality*: La Paz, Lower California, Mexico, in the tidal zone.

*Range*: La Paz to Tangola-Tangola Bay, Mexico.

*Collecting Station*: Mexico: Tangola-Tangola Bay (196-D-6, 7), 6-7 fathoms, sand, crushed shell.

*Description*: The specimen which we have referred to *Solen pazensis* is oblong with anteriorly terminal beaks, the anterior extremity is rather steeply truncated and the posterior end is rather squarely truncated but rounded at the dorsal and ventral margins. The periostracum is of a shiny horn color. There are darker blotches on the anterior ends and a darker triangle is bounded by a line which runs from the anterior dorsal to the posterior ventral margin. This triangle is not so pronounced on the present specimen as that shown on the figure given by Lowe. Dark purplish bands of color occur parallel to the lines of growth and the interior of the shell is purplish. The specimen measures approximately: length, 31 mm.; height, 7.6 mm.; convexity (both valves together), 4 mm.

This species is very similar to *Solen pfeifferi* Dunker which was described from Ecuador. The measurements of the present specimen indicate a greater height in proportion to the length in comparison to specimens of *S. pfeifferi* in the present collection. However, the measurements given for the type specimens of the two species differ but little. The main difference mentioned in the original description of *S. pazensis* is in the color but on the present specimen this does not differ much from that of *S. pfeifferi*. It is possible that *S. pazensis* is only a northern form or subspecies of *S. pfeifferi* but from the specimens available at the present time we are not able definitely to determine the relationship of the two.

*Distribution*: A single specimen referred to this species was dredged by the expedition in Tangola-Tangola Bay, Mexico, in 6-7 fathoms. This is an extension south of the known range of this species.

### **Solen pfeifferi** Dunker.

Plate I, Fig. 2.

*Solen pfeifferi* Dunker, *Proc. Zool. Soc. London*, December 10, 1861, p. 420. "Hab. Caraccas, West Columbia (H. Cuming)."—Sowerby, Conch. Icon., Vol. 19, *Solen*, June, 1874, species 26, pl. 6, fig. 26. "Hab. Bay of Caraccas." — Clessin, Conchyl.-Cab. von Martini-Chemnitz, Bd. 11, Abt. 3, Solenacea, 1888, p. 29, Taf. 12, fig. 6. Original locality cited.

*Type Locality*: Caraccas, Ecuador.

*Range*: Tangola-Tangola Bay, Oaxaca, Mexico, to the Bay of Caraccas, Ecuador.

*Collecting Stations*: Mexico: Tangola-Tangola Bay (196-D-13), 10 fathoms, gr. sand, crushed shell; Nicaragua: Corinto (200-D-10, 11, 16, 19), 4-13 fathoms, mangrove leaves, sand, also on beach.

*Description*: "Testa linearis, brevis, paullo curvata, solidula, convexa, alba, area zonis fulvis picta; margines dorsi et basis exacte paralleli, aliquantulum curvati, extremitas antica oblique truncata, sulcata, supra et infra obtusa; extremitas postica rotundato-truncata, margini antico subparallela; epidermis olivacea." "Species parva, callosa, 52 mm. longa, 10 alta, 7 lata." (Original description).

Specimens in the present collection agree with Sowerby's illustration of *Solen pfeifferi*. They are straight, banded with purple, the anterior end is obliquely truncated and the posterior end is rather abruptly truncated. The largest specimen, a right valve, measures: length, 35 mm.; height, 7.2 mm.; convexity (one valve), 2.2 mm. A smaller specimen measures 25.4 mm. in length and 5.6 mm. in height.

The type specimen of *Solen pazensis* Lowe measured: length, 57.5 mm.; height, 11.5 mm. Other than differences in color there seems to be but little to aid in separating that species from *S. pfeifferi*.

Compared to *Solen rosaceus* the shell of *Solen pfeifferi* is higher in proportion to the length, the posterior end is less rounded and it is colored by purple bands rather than light rose.

*Solen oerstedii* Mörch[23] was described from Puntarenas, Costa Rica. It has not been illustrated but according to the description the umbonal area is colored red and the dimensions given were, length 69 mm. and height 11 mm. The species was said to be analogous to *Solen tehuelchus* d'Orbigny of Patagonia.

*Distribution*: Specimens of this species, nearly all single valves, were taken, but not abundantly, at Tangola-Tangola Bay, Mexico, and at Corinto, Nicaragua. This is an extension north of the known range of this species. Dautzenberg[24] recorded some poorly preserved specimens, questionably referable to this species, from two localities in Venezuela. We are uncertain what species is represented by those records.

### **Solen rosaceus** Carpenter.

*Solen ?sicarius*, var. *rosaceus* Carpenter, *Rept. Brit. Assoc. Adv. Sci.* for 1863 (issued August, 1864), pp. 536, 638. Cited from the vicinity of Santa Barbara and the region between San Pedro and San Diego, California. Reprint in *Smithson. Miscell. Coll.*, No. 252, 1872, pp. 22, 124.—Carpenter, *Ann. & Mag. Nat. Hist.*, Ser. 3, Vol. 15, March,

[23] *Solen oerstedii* Mörch, *Malakozool. Blätter*, Bd. 7, December, 1860, p. 183. "Puntarenas." Costa Rica.

[24] *?Solen pfeifferi* Dunker, Dautzenberg, *Mem. Zool. Soc. France*, Vol. 13, 1900, p. 252.

1865, p. 177. "Hab. Sta. Barbara (Jewett); S. Pedro (Cooper)." Reprint in *Smithson. Miscell. Coll.*, No. 252, 1872, p. 279.

*Solen rosaceus* Carpenter, Weymouth, *Calif. Fish & Game Comm., Fish Bull.*, No. 4, 1920, p. 50, pl. 15, fig. 3. San Diego, California.—Johnson & Snook, Seashore Anim. Pac. Coast (Macmillan Co., New York), 1927 (also ed. 1935), p. 458, figs. 456 and 457. It burrows in the mud of bay shores from Santa Barbara, California, to the Gulf of California.

*Type Locality*: Santa Barbara, California (cited as type locality by I. S. Oldroyd in 1924 and accepted as such by the present authors). Also cited originally as occurring in the region between San Pedro and San Diego, California.

*Range*: Santa Barbara, California, to Punta Penasco, Sonora, in the Gulf of California, and south to Mazatlan, Sinaloa, Mexico.

*Collecting Stations*: Mexico: Cape San Lucas, Lower California; San Lucas Bay (135-D-25), 7 fathoms, sand; [?] Santa Inez Bay (145-D-1, 3), 4-13 fathoms, sand.

*Description*: The original description, a comparison with *Solen sicarius* Gould, follows: "Straight, narrower, longer, smaller; glossy, rosy." The shell of *Solen rosaceus* is more cylindrical, the anterior extremity is more rounded, and it is longer and narrower than that of *S. sicarius*.

A specimen from Cape San Lucas measures: length, 47.5 mm.; height, 9 mm.; convexity (both valves together), 6 mm. Large specimens of this species attain a length of about 75 mm. according to Johnson & Snook.

According to Weymouth "It is interesting as being capable of a kind of 'swimming' though habitually found in burrows."

*Solen tanozawaensis* Nomura,[25] described from the lower Miocene of Japan, is less arcuate dorsally than *S. rosaceus* to which species it was compared.

*Distribution*: Only a few specimens, one or two at a locality, were collected in the Cape San Lucas region and one doubtfully identified as this species in Santa Inez Bay. It burrows in the mud of bay shores and on sand flats from Santa Barbara, California. to Punto Penasco, Sonora, Mexico, in the Gulf of California, and south to Mazatlan, where it was collected by the senior author. It has been recorded from Miocene to Recent in California and in the Pleistocene in Lower California.

### Genus **Ensis** Schumacher.

#### **Ensis californicus** Dall.

*Ensis californicus* Dall, *Proc. U. S. Nat. Mus.*, Vol. 22, No. 1185, October 9, 1899, p. 110. "Specimen from 14 fathoms, sand, off the island of San Pedro Martir, Gulf of California." — I. S. Oldroyd, *Stanford Univ. Publ. Univ. Ser. Geol. Sci.*, Vol. 1, 1924, p. 189, pl. 49, fig. 6. Type locality cited. Range, Monterey Bay, California, to the Gulf of California.

*Type Locality*: Off the island of San Pedro Martir, Gulf of California, in 14 fathoms, sand.

*Range*: Monterey, California, to the Gulf of California and south to Manzanillo, Mexico.

*Collecting Station*: Mexico: Manzanillo (184-D-2), 30 fathoms, gravelly sand.

*Description*: Shell small, slender, arcuate, the sides nearly parallel, the valves being slightly attenuated toward the ends, beaks anterior, the anterior truncation bluntly rounded, the posterior similar; color white with livid pink streaks concentrically disposed; epidermis olivaceous brilliantly polished; hinge with small and very delicate cardinals (usually broken off), one in the right and two in the left valve, the dorsal ridge comparatively strong and elevated, shorter than the ligament. Length of shell, 60 mm.; of dorsal tooth or ridge, 5.2 mm.; of ligament, 9 mm.; width of shell, 7 mm.; perpendicular to the chord of the arc formed by the dorsal margin of the valves, 2 mm. (Dall).

The present specimen, a left valve, measures approximately: length, 60.5 mm.; height, 7.3 mm.; convexity (one valve), 2 mm.

Compared to the east American *Ensis minor* Dall,[26] the west coast shell is smaller when adult, wider in front than posteriorly, and the valves are less arcuate and proportionately narrower.

*Distribution*: A single left valve of *Ensis californicus* was dredged by the expedition at Manzanillo, Mexico, in 30 fathoms on a sandy bottom. This is an extension south of the known range of the species.

### Genus **Solecurtus** Blainville.

Key to the species of *Solecurtus*.

A. Obliquely sculptured posteriorly only; periostracum black ........................ *broggii*

B. Obliquely sculptured both posteriorly and and in greater part anteriorly; periostracum yellowish-brown ........... *guaymasensis*

#### **Solecurtus broggii** Pilsbry & Olsson.

*Solecurtus broggii* Pilsbry & Olsson, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 93, September 9, 1941, p. 71, pl. 18, fig. 4. "Jama formation, Puerto Jama. Also recent, the Type, A.N.S.P. 175547, from Callo, Port of Jipijapa, Ecuador."

*Type Locality*: Callo, port of Jipijapa, Ecuador.

*Range*: Gulf of Chiriqui, Panama, to Ecuador and northern Peru.

*Collecting Station*: Panama: Gulf of Chiriqui (221-D-1, 5), 35-40 fathoms, sandy mud.

[25] *Solen tanozawaensis* Nomura, *Saito Ho-On Kai Mus. Res. Bull.*, No. 6, September, 1935, p. 64, pl. 7 (6), fig. 3. "Tanozawa (near railroad station) Odose-mura." Nisi-Tugaru district, Aomori-ken, northeast Honsyû, Japan. Lower Miocene.

[26] See *Ensis minor* Dall, Perry, *Bull. Amer. Paleo.*, Vol. 26, No. 95, August 12, 1940, p. 81, pl. 17, fig. 112. Southwest Florida. In sandy bottoms—on sand bars in shallow water and at moderate depths.

*Description*: Shell rather large, broadly soleniform, moderately convex, with a wide, open, posterior gap; dorsal and ventral margins parallel, nearly straight, the anterior end rounded, the posterior flatly rounded to subtruncate; umbones not prominent, with the small beak a short distance behind the front third of the length. Surface marked with lines of growth except on the posterior area where, in addition, there is a series of spaced, irregular lines which cross the shell vertically and bend obliquely forward near their lower ends. There are also faint, wide, depressed rays radiating from the umbones to the ventral margin, fom the vertical of the beaks backward. Interior of right valve with a deep, wide, pallial sinus reaching to a point forward of the line of the beaks; anterior adductor scar fairly distinct, situated well into the interior of the valve in its dorsal portion. Hinge with a large, erect, hook-shaped cardinal tooth, preceding a small, oblique pit of the resilium and a large, thick, erect plate for the attachment of the ligament. (In life the shell is covered with a black epidermis). Length, 84 mm.; height, 33 mm.; semidiameter 10.3 mm. Type. (Original description).

A right valve in the present collection dredged in the Gulf of Chiriqui, Panama, measures: length, 35.5 mm.; height, 15 mm.; convexity (one valve), 4.8 mm.

This specimen is thicker, longer in proportion to the length, and the oblique sculpture is more distantly spaced and more nearly vertically inclined in comparison to that of specimens of *Solecurtus guaymasensis* of the same size. Oblique sculpture on the present specimen is present a little farther anteriorly than that shown on the illustration of the type specimen of *Solecurtus broggii* but the general features of our shell suggest its identity with that species.

*Solecurtus gatunensis* Toula,[27] described from the Gatun Miocene of Panama, is a very similar species. It also is said to lack oblique sculpture on the anterior half of the shell.

*Distribution*: A single valve of this species was dredged in the Gulf of Chiriqui, Panama, in 35-40 fathoms. This is an extension north of the known range of the species. It also has been recorded as occurring in the Pliocene of Ecuador and in the Pleistocene of Panama.

### *Solecurtus guaymasensis* Lowe.

*Psammosolen guaymasensis* Lowe, *Trans. San Diego Soc. Nat. Hist.*, Vol. 8, No. 6, March 21, 1935, p. 18, pl. 1, fig. 7. "Guaymas, 20 fathoms." Type. Also from . . . "off Angel de la Guardia Island, Gulf of California."

*Type Locality:* Guaymas, Sonora, Mexico, in 20 fathoms.

*Range:* Cedros Island, Lower California, to Angel de la Guardia Island, Gulf of California, and south to the Gulf of Chiriqui, Panama.

*Collecting Stations:* Mexico: East of Cedros Island (126-D-2, 8-11, 17), 38-60 fathoms, mud, crushed shell, eel grass; Cape San Lucas, Lower California; Panama: Gulf of Chiriqui (221-D-1, 5), 35-40 fathoms, sand, mud.

*Description:* Shell subcylindric, broadly soleniform, gaping at both ends, beaks not prominent, situated at about one-third the length of the shell from the anterior end; white under a thin, yellowish-brown periostracum, usually absent near the beaks but closely adherent toward the edges; anterior end evenly rounded, the posterior end somewhat obliquely rounded, basal margin straight, posterior dorsal margin straight, anterior dorsal margin gently sloping especially on young shells but on some specimens, especially on large shells, it is nearly straight; exterior surface sculptured with rather indistinct lines of growth and fine, raised lines resembling overlapping clapboard structure which cross the shell, posteriorly approaching a vertical but quite oblique toward the anterior end; on the anterior and posterior ends the adult shell is ornamented with faint radiating striae; ligament external, strong, attached to a projecting nymph; hinge of right valve with a sharp, curved, projecting tooth directly under the beak, posterior to which there is a flattened erect process against which there is fitted a broad, hooked tooth in the left valve; pallial sinus fairly wide extending slightly past a line vertical with the beaks, descending a little toward the end which is elliptically rounded, for about half its length below, it is confluent with the pallial line.

A large specimen dredged east of Cedros Island measures: length, 55.6 mm.; height, 23 mm.; convexity (both valves together), 17 mm.; pallial sinus extends forward 38 mm. from the posterior end of the shell.

The anterior dorsal margin of young specimens slopes decidedly from the beak but this appears to be a variable character. Large specimens in the collection of the California Academy of Sciences which were collected by Woodbridge Williams at Arena Point, Lower California, have the anterior dorsal margin nearly straight. Miss Viola Bristol of the San Diego Society of Natural History kindly compared some of our specimens with the type and paratype of "*Psammosolen*" *guaymasensis* Lowe. She stated that the type specimen is an old, thickened shell on which the anterior dorsal margin is approximately straight. Furthermore the oblique sculpture consists of more numerous lines than the original illustration shows and that these are not incised lines but rather offset or clapboard ornamentation. Young specimens in the present collection were said to be identical with Lowe's paratype. For these reasons we have identified our specimens with *Solecurtus guaymasensis* rather than considering them to be referable to *S. broggii*.

*Solecurtus broggii* Pilsbry & Lowe, described from Ecuador, is ornamented, mostly

[27] *Solecurtus gatunensis* Toula, Jahrb. K. K. Geol. Reichsanst., Bd. 58, Heft 4, 1908 (1909), p. 732 (60), pl. 28 (4), fig. 12. "von Gatun am Panama-Kanal." Miocene.

on the posterior part of the shell, by more widely spaced and more vertically inclined sculpture.

The present species apparently bears only a general similarity to such species as *Solecurtus vicksburgensis* Aldrich[28] from the Vicksburg Oligocene of Mississippi, and *"Psamosolen" aldrichi* Gardner[29] from the Miocene of Florida. *Solecurtus cumingianus* Dunker is another species which occurs in the Pliocene of Florida. *Solecurtus sanctaemarthae* which occurs in Caribbean waters is much higher in proportion to the length in comparison to *S. guaymasensis*.

*Distribution:* Specimens of this species were dredged by the expedition east of Cedros Island, Lower California, to the Gulf of Chiriqui, Panama, in 35-60 fathoms. The present records of occurrence extend the known range of the species both to the north and to the south.

## SUPERFAMILY MACTRACEA.

### Family Mactridae.

A number of generic, subgeneric and specific names have been applied to the Mactridae by various workers. These distinctions are based for the most part on the hinge characters. Unless shells are in perfect condition some of the small laminae in the hinge are difficult to observe or may be missing entirely. Discussions of the hinge characters of this family by Dall[30] as well as the discussion and excellent drawings of hinges by Lamy[31] are of great assistance in a study of the Mactridae.

Key to the genera and subgenera of the Mactridae.

A. Shell partly or entirely concentrically undulated or wave-plaited
- a. Wave-plaited on beaks only (or partly so, occasionally lacking) ... *Micromactra*
- aa. Entire shell concentrically undulated
  - b. Posterior end very elongate *Raëta*
  - bb. Posterior end short
    - c. Posterior angulation with a lamina or keel
      - d. Anterior laterals well developed ........... *Mactrinula*
      - dd. Anterior laterals very short ... *Harvella*
    - cc. Posterior angulation without a lamina or keel ... *Tumbeziconcha*[32]

B. Shell smooth or concentrically threaded, not undulated
- a. Ligament partly external
  - b. Chondrophore set off from ligament by a shelly lamina
    - c. Posteriorly rostrate ... *Anatina s.s.*[32]
    - cc. Ovately trigonal or elongate
      - d. Shell ovately elongated; impressed fasciole on posterior dorsal area with darker periostracum .... *Mactrotoma*
      - dd. Shell ovately trigonal
        - e. Thin; posterior lateral teeth short .... *Mactrella*
        - ee. Thick; posterior lateral teeth long.. *Mactra s.s.*[32]
  - bb. Chondrophore not set off from ligament by a shelly lamina .. *Spisula*[32]
- aa. Ligament entirely internal ...... *Mulinia*

Genus **Mactra** Linnaeus.

Subgenus **Mactrotoma** Dall.

**Mactra (Mactrotoma) nasuta** Gould.

Plate II, Fig. 12.

*Mactra nasuta* Gould, *Proc. Boston Soc. Nat. Hist.*, Vol. 4, November, 1851, p. 88. "Mazatlan, Lieut. Green; San Pedro, Maj. Rich."—Packard, *Univ. Calif. Publ. Bull. Dept. Geol.*, Vol. 9, No. 15, May 1, 1916, p. 278, pl. 12, figs. 2a, 2b, 2c. San Pedro, California. Range, San Pedro, California, to west Colombia (Dall).

*Mactra (Spisula) fragilis* Chemnitz, Carpenter, Cat. Mazatlan Shells, September, 1855, p. 51. [Record from Mazatlan, only].

Not *Mactra fragilis* Chemnitz = *Mactra brasiliana* Lamarck. Caribbean region.

*Type Locality*: Mazatlan, Mexico.

*Range*: San Pedro, California, to west Colombia.

*Collecting Stations*: Mexico: Arena Bank (136-D-16, 30), 30-45 fathoms, muddy sand, sand, weed; Colombia: Gorgona Island, shore.

*Description*: Shell solid, transverse, ovately cuneate, white, periostracum straw-colored, posteriorly thickened and darkened; beaks nearly median, acute; anterior side narrow, compressed, gently sloping; posterior side wider, truncated, gaping; posterior dorsal area lanceolate, excavated; interior polished, white; ligamental pit very oblique; tooth V-shaped, thin, elongated; lateral teeth thickened. Long. 3¼; lat. 1; alt. 2¼ poll. (Free translation of Gould's original description).

The analogue of *M. brasiliana*, distinguished by the posterior position of the beaks and the more attenuated form of the

[28] *Solecurtus vicksburgensis* Aldrich, *Cincinnati Jour. Nat. Hist.*, Vol. 8, July, 1885, p. 145, pl. 2, fig. 1. Vicksburg, Mississippi. Oligocene.

*Psamosolen vicksburgensis* Aldrich, Gardner, *U. S. Geol. Surv., Prof. Paper* 142-E, 1928, p. 216, pl. 33, fig. 1.

[29] *Psamosolen aldrichi* Gardner, *U. S. Geol. Surv., Prof. Paper* 142-E, 1928, p. 216, pl. 33, figs. 2 and 3. "1 mile below Baileys Ferry, Chipola River, Calhoun County, Fla." "Chipola formation." Lower Miocene.

[30] Dall, W. H. Synopsis of a Review of the Genera of Recent and Tertiary Mactridae and Mesodesmatidae. *Proc. Malacol. Soc. London*, Vol. 1, No. 5, March, 1895, pp. 203-213.—Dall, W. H., *Trans. Wagner Free Inst. Sci.*, Vol. 3, Pt. 4, April, 1898, pp. 862-891. See also Dall, W. H. Synopsis of the Mactridae of Northwest America, South to Panama. *Nautilus*, Vol. 8, No. 4, August, 1894, pp. 39-43.

[31] Lamy, E. Révision des Mactridae vivants du Muséum d'Histoire Naturelle de Paris. *Journ. de Conchyl.*, Vol. 63, No. 3, November 30, 1917, pp. 173-275, pl. 6, 8 figs. in text; No. 4, February 28, 1918, pp. 291-411, pl. 7, 22 figs. in text. See also Tomlin, J. R. leB., *Jour. Conch.*, Vol. 17, No. 5, July, 1924, pp. 134-136.

[32] Not represented in the present collection.

anterior half caused by the concave outline of the dorsal margin. The parts composing the hinge are more oblique (Gould).

Specimens in the present collection agree so perfectly with Gould's original description of *Mactra nasuta* that we have referred them to that species. The submedian position of the beaks, the tapering and roundly pointed anterior end, the truncated posterior end and the lanceolate posterior area bounded by two ridges between which the periostracum becomes thickened and darker are characteristic features of this species. The pallial sinus is rounded at the end and projects forward about two-fifths the length of the shell and is free from the pallial line below. On some specimens, especially large ones, a faint median angulation occurs from the umbos to the ventral margin. The largest specimen in the present collection, a right valve from Gorgona Island, Colombia, measures approximately: length, 118.5 mm.; height, 82 mm.; convexity (one valve), 20.5 mm.; pallial sinus extends anteriorly 47 mm. from the posterior margin of the shell.

Gould[33] in 1853 stated regarding *Mactra nasuta*: "This species, described in Proceedings Bost. Soc. Nat. Hist., Nov., 1851, IV, 88, agrees so nearly with *M. falcata*, also described by me, (op. cit. III. 216,) that I hesitate to reproduce it as new without a direct comparison of the two shells, which I have it not now in my power to make. They will for the present, therefore, be regarded as synonymous. *M. falcata*, however, was found at Puget's Sound, while *M. nasuta* was found by Maj. Rich at San Pedro, and by Lieut. Green, (with a doubt,) at Mazatlan."

These later remarks of Gould do not appear to be in conformity with those given at the time of the original description where it was stated that *Mactra nasuta* is the analogue of *Mactra brasiliana* Lamarck,[34] a statement which is true of the present specimens here referred to *M. nasuta*. Gould's remarks in 1853 seem applicable to *Mactra planulata* Conrad[35] or to *Mactra dolabriformis* Conrad,[36] or the generally more northern *M. falcata* Gould.[37] However, it is true that at the time of the original description of *Mactra falcata* Gould, from Puget Sound, he compared it to *M. brasiliana* and *M. ovalis*.

*Mactra dolabriformis* Conrad (the smaller of Conrad's figures, 1869), described from Panama, bears a resemblance to *M. planulata* but is quite distinct. It can be separated from *M. planulata* by the more attenuated form anteriorly, the anterior dorsal margin beneath the beaks is more projecting and in adult shells there is a narrow radial depression anterior to the posterior angulation. Interiorly the pallial sinus is much wider, slightly longer, and joins the posterior adductor impression considerably above the base while in *M. planulata* it joins the adductor impression at or near the base and extends forward in nearly a straight line. The ventral margin of the hinge plate in *M. dolabriformis* forms nearly a straight line while in *M. planulata* it is decidedly curved around the chondrophore. The interior of *M. dolabriformis* is smooth while that of adult specimens of *M. planulata* is marked by irregularities radiating from under the umbos.

The general shape of *Mactra falcata* is similar to that of *M. dolabriformis* but it is more elongate in proportion to the height. The dorsal area both anteriorly and posteriorly is narrower and not upturned at the edges as it is in *M. dolabriformis*. Furthermore the lunule-like area on *M. dolabriformis* is long, lanceolate and delimited by a subangulation. On *M. falcata* this area is somewhat depressed but not sharply delimited except just below the beaks. The pallial sinus of *M. falcata* is similar to that of *M. planulata* in that it extends forward from near the base of the anterior adductor impression but it is slightly wider and longer than in Conrad's species.

This group of closely related species has been discussed by Burch[38] and others. Burch placed *Mactra dolabriformis, M. falcata, M. hemphilli* and *M. planulata* under the genus *Spisula*.

Dall[39] was of the opinion that the species described as *Mactra californica* by Reeve[40] and Deshayes and later named *Mactra deshayesi* by Conrad could be referred to *Mactra nasuta*. The figure given by Reeve is not at all typical of *M. nasuta*. Grant & Gale mentioned that in some cases specimens of young *Schizothaerus nuttallii* Conrad have been mistakenly referred to *M. nasuta*. It seems quite possible that this may be true in the case of the species described by Reeve as *M. californica*. *Mactra hiantina* Deshayes,[41] an unfigured species described from

---

33 Gould, A., *Boston Jour. Nat. Hist.*, Vol. 6, October, 1853, p. 393.

34 See *Mactra fragilis* Chemnitz, Reeve, Conch. Icon., Vol. 8, *Mactra*, 1854, species 47, pl. 11, fig. 47. Honduras. Also *Mactra (Mactrotoma) fragilis* Chemnitz, Lamy, *Journ. de Conchyl.*, Vol. 63, No. 3, 1917, p. 246, pl. 6, figs. 5 and 7. [With synonymy].

35 *Mactra planulata* Conrad, *Jour. Acad. Nat. Sci. Philadelphia*, Vol. 7, 1837, p. 240. "Inhabits with the former" [that is *M. californica* which "Inhabits muddy marshes, bare at low water, near Sta. Barbara; rare."]

*Spisula falcata* Gould, Packard, *Univ. Calif. Publ. Bull. Dept. Geol.*, Vol. 9, No. 15, May 1, 1916, pl. 26, figs. 1a, 1b, 1c. Not *Mactra falcata* Gould.

36 *Spisula dolabriformis* Conrad, *Amer. Jour. Conch.*, Vol. 3, Pt. 2, September 5, 1867, p. 193. "Inhabits Panama." [Described as "*Spissula*" *dolabriformis* but corrected to *Spisula dolabriformis* in Ap. p. 44].—Conrad, *Amer. Jour. Conch.*, Vol. 5, Pt. 2, 1869, p. 108, pl. 12, fig. 1. [Smaller figure only. The larger figure showing the hinge appears to represent *M. hemphilli* Dall or a similar form].

37 *Mactra falcata* Gould, *Proc. Boston Soc. Nat. Hist.*, Vol. 3, May, 1850, p. 216. "Hab. Puget Sound, Oregon." —Gould, U. S. Explor. Exped., Atlas, Moll., 1856, pl. 34, figs. 506, 506a, 506b.—I. S. Oldroyd, *Stanford Univ. Publ. Univ. Ser. Geol. Sci.*, Vol. 1, 1924, p. 195, pl. 20, figs. 1, 2, 3. [Copies of Gould's figures 506 and 506b.].

38 See *Min. Conch. Club. South. Calif.*, No. 44, February, 1945, pp. 17-18.

39 Dall, W. H., *Nautilus*, Vol. 8, No. 4, August, 1894, p. 39.

40 *Mactra californica* Reeve, Conch. Icon., Vol. 8, *Mactra*, May, 1854, species 114, pl. 20, fig. 114. "Hab. California." —Deshayes, *Proc. Zool. Soc. London* for 1854 (issued February 10, 1855), p. 68. "Hab. Gulf of California. Coll. Cuming." Not *Mactra californica* Conrad.

41 *Mactra hiantina* Deshayes, *Proc. Zool. Soc. London* for 1854 (issued February 10, 1855), p. 68. "Hab. Puna, Guayaquil."

Ecuador, was placed in the synonymy of *M. nasuta* by Dall. He also referred "*M. ovalina* Auct. not Lam." (see Reeve's pl. 14, fig. 66 "Hab. West Columbia; Cuming.") to *M. nasuta*. Lamy[42] considered Lamarck's species illustrated by Reeve to be referable to *Mactra depressa* Spengler which occurs in the western Pacific.

*Distribution*: Two valves of *Mactra nasuta* were dredged by the expedition in 30-45 fathoms on Arena Bank in the Gulf of California and one valve was collected on the beach at Gorgona Island, Colombia. We have seen a specimen from Newport Beach, California, but the species apparently occurs but rarely as far north as southern California. It also has been cited as occurring in the upper Pleistocene of the San Pedro region by De Long.[43]

### Subgenus **Micromactra** Dall.

Key to the species of *Micromactra*.

A. Pallial sinus extending to or past a line vertical with the beaks
  - a. Shell high, height 68 to 70 per cent. of the length ........................ *isthmica*[44]
  - aa. Shell elongate, height 63-65 per cent. of the length ........................ *fonsecana*

B. Pallial sinus not extending to a line vertical with the beaks
  - a. Anterior dorsal margin concave; thin *angusta*
  - aa. Anterior dorsal margin nearly straight
    - b. Beaks entirely or partly wave-plaited
      - c. Wave-plaited over entire beaks *californica*[44]
      - cc. Wave-plaited only on posterior curve of beaks ............ *vanattae*
    - bb. Beaks not wave-plaited. *acymata*[44]

### **Mactra (Micromactra) angusta** Reeve.

Plate II, Figs. 14 & 18.

*Mactra angusta* Reeve, Conch. Icon., Vol. 8, *Mactra*, May, 1854, species 93, pl. 18, fig. 93. "Hab. Panama. Cuming."—Deshayes, *Proc. Zool. Soc. London* for 1854, p. 67 (issued February 10, 1855. "Hab. Panama. Coll. Cuming."—Weinkauff, Conchyl.-Cab. von Martini-Chemnitz, Bd. 11, Abt. 2, *Mactracea*, 1884, p. 70, Taf. 25, figs. 2, 2a. Panama.

*Type Locality*: Panama.

*Range*: Champerico, Guatemala, to Zorritos, Peru.

*Collecting Stations*: Guatemala: 7 miles west of Champerico (197-D-1, 2), 14 fathoms, mud; El Salvador: La Libertad (198-D-1, 2), 13-14 fathoms, mud.

*Description*: Shell ovately transverse, narrow, rather triangular, nearly equilateral, compressed, white, thin, fragile, transversely regularly striated, anterior side a little the shorter, obtuse, rather concave at the upper part, posterior side slanting at the upper part, attenuated; area narrow, elongated, flat, with a ridge on each side; umbos very small, a little oblique, regularly wave-plaited; lunule very small, lanceolate. (Original description).

The pallial sinus is broadly rounded at the end and extends to about three-sevenths the length of the shell, usually only the posterior portion confluent with the pallial line below or sometimes almost wholly free.

The largest specimen in the present collection, a right valve from off Guatemala, measures: length, 42 mm.; height, 26.6 mm.; convexity (one valve), 6.5 mm.; pallial sinus extends anteriorly 20.3 mm. from the posterior margin of the shell.

Specimens in the present collection agree exactly with Reeve's original figure and description of *Mactra angusta*. These are characterized by the thin, white, fragile shell, concentrically wave-plaited on the umbos, and with a decided concavity in the anterior dorsal margin below the beaks.

The shell illustrated under the name of *Mactra angusta* by Pilsbry & Lowe represents a different shell which lacks the concavity in front of the beaks, and has the anterior end less broadly rounded, the posterior end broader and the pallial sinus longer. It is described in the present paper under the name of *Mactra* (*Micromactra*) *fonsecana*.

The more elongate outline and the concave margin in front of the beaks are features which serve as an aid in separating *Mactra angusta* from *Mactra californica* Conrad, a more northern species.

Some of the other described forms of the *Mactra angusta* group belonging to *Micromactra* are the following: *Mactra macescens* Guppy, 1866, from the Miocene of Trinidad; *M. macescens haasi* Hertlein & Strong [= *M. macescens elongata* Haas[45]], Miocene of Costa Rica; *M. iridia* Olsson, 1932, Miocene of Peru; *M. atacama* Pilsbry & Olsson, 1941, Pliocene of Ecuador. Forms similar to *M. californica* are: *M. californica maracaibensis* H. & K. Hodson, 1931, Miocene of Venezuela; *M. californica onnechiura* Otuka, 1937, mid-Tertiary of Japan; *Mactra janeiroensis* E. A. Smith, 1915, off Rio de Janeiro, Brazil; and perhaps *M. tholoensis* Ladd, 1934, Neogene of Fiji.

*Distribution*: Specimens of *Mactra angusta* were dredged by the expedition off Guatemala and El Salvador at depths of 13-14 fathoms on a mud bottom. This is an extension north of the known range of the species. Species of this group occurred on both sides of Central America during the Miocene.

---

[42] Lamy, E., *Journ. de Conchyl.*, Vol. 63, No. 3, 1917, p. 255.

Nomura (*Sci. Repts.* Tohoku Imper. Univ., Sendai, Japan, Ser. 2, (Geol.), Vol. 15, No. 2, 1932, p. 91 (27), cited *M. ovalina* as occurring both fossil and Recent in Japan.

[43] De Long, Jr., J. H., *Trans. San Diego Soc. Nat. Hist.*, Vol. 9, No. 25 1941, opp. p. 244.

[44] Not represented in the present collection.

[45] *Mactra* (*Micromactra*) *macescens* Guppy var. *elongata* Haas, *Jour. Paleo.*, Vol. 16, No. 3, May, 1942, p. 313, text fig. 1. (p. 314). "Probably Carballo, Costa Rica, middle Miocene." Not *Mactra elongata* Quoy & Gaimard, 1835.

The new subspecific name *haasi* is here proposed for the form described by Haas.

### *Mactra (Micromactra) fonsecana*

Hertlein & Strong, sp. nov.

Plate II, Figs. 16, 19 & 20.

*Mactra* (*Micromactra*) *angusta* Deshayes, Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 84, May 21, 1932, p. 89, pl. 15, figs. 3, 4; pl. 16, fig. 3. "Panama" and "Montijo Bay."

Not *Mactra angusta* Reeve, 1854.

Shell elongate, white covered by a brownish-gray periostracum, moderately compressed, gaping widely behind and slightly so in front, lunular region and escutcheon flattened; anterior dorsal margin nearly straight from beaks to the broadly rounded anterior end which merges into the very broadly rounded ventral margin, posterior end obliquely subtruncated; umbos concentrically wave-plaited in front and behind but only faintly so in the middle; the remainder of the shell is ornamented with concentric threads and the posterior area is set off by two or three irregular radial threads; hinge typical for the subgenus; interior smooth, white; pallial sinus long, rounded at the end, projecting for about two-thirds the length of the shell and for most of its length confluent with the pallial line. Length, 53.2 mm.; height, 34.5 mm.; convexity (both valves together), 17.5 mm.; pallial sinus extends anteriorly 32 mm. from the posterior margin of the shell.

Holotype in California Academy of Sciences Paleontology Type Collection, from Potosi and Monypenny Point, Nicaragua, Gulf of Fonseca. Paratypes from the same locality. A paratype from Panama Bay was collected by F. M. Anderson.

Additional specimens were taken by the expedition at the following stations: 7 miles west of Champerico, Guatemala (197-D-2), 14 fathoms, mud; Meanguera Island, Gulf of Fonseca, El Salvador (199-D-1), 16 fathoms, mud; Corinto, Nicaragua, beach.

The shell of this species differs from that of *Mactra angusta* in the nearly straight anterior dorsal margin, rather than excavated in the lunular area, in the broader subtruncated posterior end and in the much longer pallial sinus.

Specimens in the collection which agree exactly with Reeve's original figure and description of *M. angusta* are quite distinct from the shell illustrated under that name by Pilsbry & Lowe.

### *Mactra (Micromactra) vanattae*

Pilsbry & Lowe.

*Mactra* (*Micromactra*) *vanattae* Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 84, May 21, 1932, p. 90, pl. 16, figs. 4, 4a, 4b. "Beach at eastern end of Panama City (Pinchot Exped., 1929). Type 155921 ANSP. La Union, Gulf of Fonseca (Lowe, 1931)."

*Type Locality*: Beach at eastern end of Panama City, Panama.

*Range*: Champerico, Guatemala, to Panama Bay.

*Collecting Stations*: Guatemala: 7 miles west of Champerico (197-D-2), 14 fathoms, mud; Nicaragua: Corinto, beach.

*Description*: Shell with outline similar to that of *Mactra californica*, fairly thick, compressed, gaping posteriorly, white under a thin grayish-drab periostracum; umbos delicately concentrically wave-plaited in front of the posterior angulation but lacking on the anterior convexity; pallial sinus elliptically rounded at the end and extending about 45 percent. the length of the shell and for most of its length confluent with the pallial line.

The largest specimen in the present collection, a left valve from off Guatemala, measures: length, 32 mm.; height, 21.8 mm.; convexity (one valve), 5.5 mm.; pallial sinus extends anteriorly 14.5 mm. from the posterior margin of the shell.

The shell of this species differs from that of *Mactra californica* in that the concentric wave-plaited sculpture is present only on the posterior portion of the umbos in front of the posterior angulation, it is thicker, the hinge plate is heavier and the posterior end is a little more truncated. The shell of this species is thicker, more elongate and lacks the concavity in the lunular area which is so pronounced on shells of *M. angusta*. The shell of *M. vanattae* is less elongate, thicker, and the pallial sinus is shorter than that of *Mactra fonsecana*.

A subspecies, *Mactra vanattae acymata* Pilsbry & Lowe[46] was described from Panama. The umbos of this subspecies are said to lack completely any concentric undulations. As pointed out by Pilsbry & Lowe it would thus technically not belong to the subgenus *Micromactra*.

*Mactra* (*Micromactra*) *isthmica* Pilsbry & Lowe[47] is somewhat similar to *M. vanattae*, but differs in that the pallial sinus extends past the middle of the shell and the height of the shell is greater in proportion to the length.

*Mactra* (*Mactroderma*) *velata* Philippi[48], which also occurs at Panama, possesses a large, thick shell on which the posterior end is evenly, rather acutely rounded rather than truncated and the posterior dorsal margin slopes more abruptly than that of *M. vanattae acymata*.

*Distribution*: Only a couple of left valves of *Mactra vanattae* were taken by the expedition off Champerico, Guatemala, and at Corinto, Nicaragua. The present record of the species from off Guatemala is an extension north of the known range of the species.

---

[46] *Mactra* (*Micromactra*) *vanattae* var. *acymata* Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 84, May 21, 1932, p. 90, pl. 16, figs. 1, 1a. "From Panama."

[47] *Mactra* (*Micromactra*) *isthmica* Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 84, May 21, 1932, p. 89, pl. 15, figs. 1, 2; pl. 16, fig. 5. "Near Panama City (J. Zetek)." Also from La Union, El Salvador, in the Gulf of Fonseca.

[48] *Mactra velata* Philippi, *Zeitschr. f. Malakozool.*, Jahrg. 5, No. 10, 1848, p. 153. "Patria: Panama."—Philippi, *Abbild. u. Beschreib. Conchyl.*, Bd. 3, Heft 8, November, 1850, p. 137 (11), pl. 3, fig. 5. Panama.—Reeve, Conch. Icon., Vol. 8, *Mactra*, 1854, species 20, pl. 5, fig. 20. "Hab. Panama (on the reef); C. B. Adams."

### Genus **Mulinia** Gray.

**Mulinia pallida** Broderip & Sowerby.

*Mactra pallida* Broderip & Sowerby, *Zool. Jour.*, Vol. 4, No. 15, January, 1829, p. 360. "Hab. ad littora Oceani Pacifici." "From St. Blas."

*Mulinia donaciformis* Gray, *Mag. Nat. Hist.*, New Ser., Vol. 1, July, 1837, p. 376. "Inhabits South Sea—Capt. Beechey's Expedition."—Sowerby, Zool. Beechey's Voy., Moll., 1839, p. 154, pl. 44, fig. 13. [Not the record "from Nevis"]. Also illustrated by Reeve, Conch. Icon., Vol. 8, *Mactra*, 1854, pl. 13, fig. 60.

*Mactra angulata* Reeve, Conch. Icon., Vol. 8, *Mactra*, April, 1854, species 34, pl. 9, fig. 34. "Hab. Gulf of California."

*Mactra carinulata* Reeve, Conch. Icon., Vol. 8, *Mactra*, April, 1854, species 38, pl. 10, fig. 38. "Hab. Gulf of California."

*Mactra goniata* Deshayes, *Proc. Zool. Soc. London* for 1854, p. 70 (issued February 10, 1855). "Hab. California."

*Mactra* (*Mulinia*) *bistrigata* Mörch, Malakozool. Blätter, Bd. 7, December, 1860, p. 182. "Realejo." Nicaragua.

*Mactra bistrigata* Mörch, Weinkauff, Conchyl.-Cab. von Martini-Chemnitz, Bd. 11, Abt. 2, Mactracea, 1884, p. 102, Taf. 34, figs. 5-7. "Vaterland: Busen von Panama (Oersted)."

*Mulinia pallida* Broderip & Sowerby, Lamy, *Journ. de Conchyl.*, Vol. 63, No. 4, 1918, p. 335. Mazatlan; Guatemala; Panama; Callao; Guayacan.

*Mactra* (*Mulinia*) *pallida* Broderip & Sowerby, Grant & Gale, *Mem. San Diego Soc. Nat. Hist.*, Vol. 1, 1931, p. 400, pl. 22, figs. 7a, 7b, 7c. Earlier records cited.

*Type Locality*: San Blas, Tepic, Mexico.

*Range*: Gulf of California to Paita, Peru.

*Collecting Stations*: Mexico: 17 miles SE. × E. of Acapulco (189-D-3), 13 fathoms, mud; Nicaragua: Corinto (200-D-19), 12-13 fathoms, mangrove leaves.

*Description*: Shell roundly trigonal, ventricose, white covered by a yellowish-olive periostracum; anterior end rounded, ventral margin broadly rounded, posterior margin sloping, nearly straight and where it joins the ventral margin acutely rounded or angulated; an angulation is present from the beak to the posterior ventral end of each valve; pallial sinus short, narrow and extending about two-fifths the length of the shell and free from the pallial line.

The specimens of this species in the present collection are small, not over 32 mm. in length. A right valve collected by the senior author at Panama Vieja (Old Panama) measures; length, 56 mm.; height, 44.5 mm.; convexity (one valve), 17 mm.; pallial sinus projects anteriorly 27.5 mm. from the posterior margin of the shell.

The shell of this species is very variable. This has caused it to receive many different specific names which are now relegated to synonymy. According to Pilsbry[49] the specimens from Panama illustrated by Li[50] under the names of "*Corbula altirostris*" and "*Corbula* cf. *swiftiana* Adams," can be referred to *Mulinia pallida*.

A very similar but somewhat more elongate form from Guaymas, Mexico, was described by Dall under the name of *Mulinia modesta*[51]. It appears to be of not more than subspecific value and may not be sufficiently distinct to merit a special name. This form occurs from Magdalena Bay to the Gulf of California. A large specimen in the collections of the California Academy of Sciences which was collected by Henry Hemphill at Magdalena Bay, Lower California, measures: length, 74.5 mm.; height, 61 mm.; convexity (both valves together), 44.5 mm.; pallial sinus projects anteriorly 33 mm. from the posterior margin of the shell.

*Distribution*: A few specimens of *Mulinia pallida* were taken by the expedition at two localities off Mexico and Nicaragua, in 12-13 fathoms. It occurs commonly from the Gulf of California to Peru. It also has been recorded as occurring in the Pleistocene of Magdalena Bay, Lower California, and in the Pliocene and Quaternary of Ecuador. According to Grant & Gale, the records of the occurrence of "*Mactra exoleta*" in the Pleistocene of southern California can be referred to *M. pallida modesta*.

### Genus **Mactrella** Gray.

#### Subgenus **Mactrella** s.s.

Key to the species of *Mactrella* s.s.

A. Shell with a strong high keel posteriorly
   a. Shell with a posterior gape .......... *clisia*
   aa. Shell without a posterior gape *subalata*[52]
B. Shell with a sharp angulation or low ridge posteriorly .......................................... *exoleta*

**Mactrella (Mactrella) clisia** Dall.

*Mactrella clisia* Dall, *Nautilus*, Vol. 29, No. 6, October, 1915, p. 62. "West coast of Mexico." Also cited as occurring from Manzanillo, west Mexico, to Santa Elena, Ecuador.—Dall, *Proc. U. S. Nat. Mus.*, Vol. 52, December 27, 1916, p. 415. "Type from Manzanillo, Mexico. Range thence to Santa Elena, Ecuador."

*Type Locality*: Manzanillo, Mexico.

*Range*: Gulf of California to Salinas, Ecuador.

*Collecting Stations*: Mexico: 17 miles SE. × E. of Acapulco (189-D-2), 20 fathoms, sandy mud, algae; Nicaragua: Corinto (200-D-19), 12-13 fathoms, mangrove leaves;

---

[49] Pilsbry, H. A., *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 83, 1931, p. 431.

[50] Li, C. C., *Bull. Geol. Soc. China*, Vol. 9, No. 3, October, 1930, p. 263, pl. 5, fig. 37 (*Corbula altirostris*); p. 264, pl. 5, fig. 39 (*Corbula* cf. *swiftiana*). Dredged in Panama Bay in 10-40 feet in mud at the mouth of the Rio Grande near La Boca about one mile from the mainland." "Horizon: Gatun formation." [Recent].

[51] *Mulinia modesta* Dall, *Nautilus*, Vol. 8, No. 1, May, 1894, p. 5, pl. 1 [lower figure]. "Habitat, Guaymas."

[52] Not represented in the present collection.

Costa Rica: Piedra Blanca, shore; Gulf of Dulce, beach; Golfito, beach.

*Description*: Shell thin, white, arcuate, attenuated and compressed anteriorly, with no circumscribed lunule, and with a small gape posteriorly; posterior slope flattened and externally bordered by a sharp angle surmounted by a thin elevated keel; pallial sinus short, sloping to a blunt rounded point which extends to about three-eighths the length of the shell and free from the pallial line.

A specimen from the Gulf of California in the collections of the California Academy of Sciences measures approximately: length, 77 mm.; height, 60.5 mm.; convexity (both valves together), 32 mm.; pallial sinus projects anteriorly 28 mm. from the posterior margin of the shell.

The shell of this species is easily separable from that of *Mactrella exoleta* by the presence of a strong elevated posterior keel.

*Mactrella alata subalata* Mörch[53] has been reported as occurring from Corinto, Nicaragua, to Santa Elena, Ecuador. According to Olsson it is a rare shell sometimes found with *M. clisia* but "it is always distinct, recognized by its longer shell and absence of the small posterior gap so characteristic of *clisia*."

*Distribution*: A few specimens, usually a single valve at a locality, were collected by the expedition at a few stations between southwest Mexico and Costa Rica.

**Mactrella (Mactrella) exoleta** Gray.

*Mactra exoleta* Gray, *Mag. Nat. Hist.*, New Ser. Vol. 1, 1837, p. 372. "Inhabits—."—Hanley, Cat. Rec. Bivalve Shells, p. 33, 1843, p. 340, 1856, pl. 11, fig. 51, 1843. "Cape Horn."—Reeve, Conch. Icon., Vol. 8, *Mactra*, 1854, species 16, pl. 4, fig. 16. "Hab. Cape Horn and West Columbia."—Carpenter, Cat. Mazatlan Shells, September, 1855, p. 50. Mazatlan, Mexico. Also earlier records cited.—Weinkauff, Conchyl.-Cab. von Martini-Chemnitz, Bd. 11, Abt. 2, Mactracea, 1884, p. 24, Taf. 8, figs. 1 and 2.—Grant & Gale, *Mem. San Diego Soc. Nat. Hist.*, Vol. 1, 1931, p. 402 (in text), pl. 22, figs. 10a, 10b. Coast of Guerrero, Mexico.

*Lutraria ventricosa* Gould, *Proc. Boston Soc. Nat. Hist.*, Vol. 4, November, 1851, p. 89. "Inhabits Mazatlan."

*Type Locality*: No locality originally cited. Corinto, Nicaragua (here designated as type locality).

*Range*: Gulf of California to Punta Picos, Peru.

*Collecting Stations*: Mexico: 17 miles SE. × E. of Acapulco (189-D-3), mud; Nicaragua: Corinto (200-D-19), 12-13 fathoms, mangrove leaves.

*Description*: Shell trigonal, white, thin, pellucid, slightly concentrically striated; covered with a thin pale periostraca; the anterior slope compressed, produced; the hinder slope ventricose, flattened, edged, with a slightly raised keel. (Original description).

The shell of this species is transversely obliquely cordate, thin, ventricose, smooth or finely concentrically striated. The anterior side is somewhat attenuated, the posterior obliquely truncated and bearing a low ridge at the angle. The pallial sinus is rather short, tapering to a bluntly rounded end which extends to about two-fifths the length of the shell and is free from the pallial line.

A large specimen from the Gulf of California in the collections of the California Academy of Sciences measures approximately: length, 121.5 mm.; height, 90.5 mm.; convexity (both valves in place), 56 mm.; pallial sinus extends anteriorly 55 mm. from the posterior end of the shell.

*Distribution*: Three small specimens of this species were dredged by the expedition southeast of Acapulco, Mexico, and off Corinto, Nicaragua, in 12-13 fathoms. It also has been reported by Olsson as occurring in the Miocene of Peru[54] and Costa Rica[55].

Subgenus **Mactrinula** Gray.

**Mactrella (Mactrinula) goniocyma** Pilsbry & Lowe.

*Mactra (Mactrinula) goniocyma* Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 84, May 21, 1932, p. 90, pl. 15, figs. 5 and 6. "Nicaragua: San Juan del Sur."—Strong, Hanna & Hertlein, *Proc. Calif. Acad. Sci.*, Ser. 4, Vol. 21, No. 10, 1933, p. 118. Acapulco, Mexico.

*Type Locality*: San Juan del Sur, Nicaragua.

*Range*: Acapulco Bay, Mexico, to La Libertad, El Salvador.

*Collecting Stations*: El Salvador: La Libertad (198-D-1, 2), 13-14 fathoms, mud.

*Description*: Shell very thin, fragile, rather compressed, ovately triangular in shape, color whitish; sculptured with oblique concentric corrugations which are angulated along a vertical from the beaks in the form of broad Vs and crossed obliquely by very fine sharp, concentric striae; a lamina occurs radiating to the posterior-basal angle and a low unornamented convexity occurs between the lamina and the posterior dorsal angle; lunular area smooth, lanceolate.

A left valve in the present collection measures approximately: length, 22 mm.; height (incomplete), 15.5 mm.; convexity (one valve), 4.5 mm.

The presence of a posterior lamina or keel serves to separate shells of the present species from those of *Mactrella (Tumbezicon-*

[53] *Mactra (Mactrella) subalata* Mörch, *Malakozool. Blätter*, Bd. 7, December, 1860, p. 180. "Realejo." [Near Corinto, Nicaragua]. Illustrated as *Mactra alata* Spengler, Reeve, Conch. Icon., Vol. 8, *Mactra*, 1854, species 29, pl. 8, fig. 29. "West Columbia; Cuming." Not *Mactra alata* Spengler, 1802. A Caribbean species.

*Mactra alata* Spengler var. *subalata* Mörch, Olsson, *Nautilus*, Vol. 48, No. 3, 1935, p. 105. Costa Rica to Santa Elena, Ecuador.

[54] *Mactra (Mactrella) exoleta* Gray, Olsson, *Bull. Amer. Paleo.*, Vol. 19, Bull. No. 68, 1932, p. 129. Upper Zorritos of Punta Picos, Peru. Miocene.

[55] *Mactra exoleta* Gray, Olsson, *Bull. Amer. Paleo.*, Vol. 9, Bull. No. 39, 1922, p. 434 (262), pl. 31 (28), fig. 2. "Gatun Stage: Boucary Creek." Costa Rica. Miocene.

*cha*) *thracioides* Adams & Reeve[56] reported from La Union, El Salvador, to Tumbez, Peru, which is ornamented only with concentric sculpture.

*Distribution*: Three left valves of *Mactra* (*Mactrinula*) *goniocyma*, somewhat imperfectly preserved, were dredged by the expedition at La Libertad, El Salvador, in 13-14 fathoms on a muddy bottom.

Subgenus **Harvella** Gray.

**Mactrella (Harvella) elegans** Sowerby.

*Mactra elegans* Sowerby, Cat. Shells Tankerville, Ap. 1825, p. II, pl. 1, fig. 3. [No locality cited].—Reeve, Conch. Icon., Vol. 8, *Mactra*, 1854, species 89, pl. 17, fig. 89. [Not the record "Hab. Florida"].—Weinkauff, Conchyl.-Cab. von Martini-Chemnitz, Bd. 11, Abt. 2, Mactracea, 1884, p. 87, Taf. 30, figs. 3, 3a.

*Harvella elegans* Sowerby, H. & A. Adams, Gen. Rec. Shells, Vol. 2, 1856, p. 378, pl. 99, figs. 4, 4a.—Chenu, Man. de Conchyl., Vol. 2, 1862, p. 56, figs. 229, 230.

*Harvella pacifica* Conrad, *Amer. Jour. Conch.*, Vol. 3, Pt. 2, September 5, 1867, p. 192. "Inhabits Panama."—Conrad, *Amer. Jour. Conch.*, Vol. 5, Pt. 2, October 7, 1869, p. 108, pl. 12, fig. 2.

*Raeta maxima* Li, *Bull. Geol. Soc. China*, Vol. 9, No. 3, October, 1930, p. 263, pl. 5, fig. 35. Dredged in " 'from 10 ft. to 40 ft. in the mud at the mouth of the Rio Grande near La Boca about one mile from the mainland in Panama Bay' ".

*Type Locality*: No locality cited originally. Panama Bay (here designated as type locality).

*Range*: Gulf of California to Zorritos, Peru.

*Collecting Stations*: Mexico: Banderas Bay, beach; El Salvador: La Union (198-D-2), 14 fathoms, mud; Costa Rica: Gulf of Dulce, beach; Panama: Gulf of Chiriqui (221-1-5), 35-40 fathoms, sandy mud.

*Description*: M. testâ rotundato-trigonâ, tumidâ, tenui, anticè acutè carinatâ, superficie eleganter concentricè sulcatâ; sulcis rotundatis. "A much rounder and more tumid shell than *Mactra plicataria*." (Original description).

The shell of *Mactrella* (*Harvella*) *elegans* is roundly trigonal, thin, white (sometimes stained brown around the margin), quite convex, concentrically undulated and ornamented with fine concentric striae as well as fine, somewhat irregular, but mostly radial wrinkles. A lamellated keel occurs along the posterior dorsal angulation. Between the keel and the steeply sloping posterior dorsal area the shell is ornamented only with concentric lines of growth, the dorsal area is somewhat concave behind the umbos. The lunular area is elongately cordate and smooth. The pallial sinus is rather narrow, rounded at the end and extends about two-thirds the length of the shell and is free from the pallial line.

A right valve of this species collected by the senior author along the beach at Panama Vieja (Old Panama), where it occurred abundantly, measures approximately: length, 61 mm.; height, 52 mm.; convexity (one valve), 20 mm.; pallial sinus projects anteriorly 39 mm. from the posterior margin of the shell. A left valve measures 64 mm. in length.

A subspecies *Mactrella elegans tucilla* Olsson[57] has been described from the Miocene of Peru. Other similar species are *Mactrella estrellana* Olsson, from the Miocene of Peru, and *M. sancti-blasii* Maury, 1925, from the Miocene of Trinidad, both of which were compared to *Mactrella* (*Harvella*) *elegans*.

*Distribution*: A few specimens of this species were collected by the expedition in the region between Banderas Bay, Mexico, and the Gulf of Chiriqui, Panama, on the beach and dredged in 14-40 fathoms, on a muddy bottom. Some of the early authors who studied this species recorded it from Florida but now it is definitely known to occur only in tropical west American waters. It has also been recorded occurring in the Miocene of Colombia[58] and De Long[59] cited it as occurring in the Palos Verdes Sands, upper Pleistocene, Signal Hill, Long Beach, California.

Genus **Anatina** Schumacher.

Subgenus **Raëta** Gray.

**Anatina (Raëta) undulata** Gould.

*Lutraria undulata* Gould, *Proc. Boston Soc. Nat. Hist.*, Vol. 4, November, 1851, p. 89. "Inhabits La Paz, Lower California."—Gould, *Boston Jour. Nat. Hist.*, Vol. 6, 1853, p. 391, pl. 15, fig. 7. La Paz, Lower California.

*Labiosa undulata* Gould, I. S. Oldroyd, *Stanford Univ. Publ. Univ. Ser. Geol. Sci.*, Vol. 1, 1924, p. 191, pl. 21, fig. 11. (Copy of Gould's figure). Type locality cited. Range, San Pedro, California, to Panama. Also Pleistocene of San Pedro and San Diego, California.

*Anatina* (*Raëta*) *undulata* Gould, Grant & Gale, *Mem. San Diego Soc. Nat. Hist.*, Vol. 1, 1931, p. 407, pl. 23, figs. 5a, 5b, 5c. Earlier records cited. Pleistocene and Recent.

*Type Locality*: La Paz, Lower California.

*Range*: San Pedro, California (Dall); Ensenada, Lower California (Burch). Scammon Lagoon, Lower California, to Kino Bay in the Gulf of California and south to Piedra Redonda, Peru.

---

[56] *Mactra thracioides* Adams & Reeve, Zool. Voy. Samarang, 1848, p. 81, pl. 23, fig. 8. "Hab. Eastern Seas."—Reeve, Conch. Icon., Vol. 8, *Mactra*, May, 1854, species 116, pl. 20, fig. 116. Eastern Seas.—Pilsbry & Olsson, *Nautilus*, Vol. 48, No. 4, 1935, pp. 120-121, pl. 6, fig. 9. Port Pizarro and the mouth of the Tumbez River, Peru. Records also cited from La Union, El Salvador, and Ecuador. *Tumbeziconcha* proposed (p. 119) with the type *Mactra thracioides* Adams & Reeve.

[57] *Harvella elegans tucilla* Olsson, *Bull. Amer. Paleo.*, Vol. 19, Bull. 68, June 30, 1932, p. 129, pl. 14, fig. 1. "Tumbez formation, Que. Tucillal at Zorritos." Peru. Miocene.

[58] *Mactrella* (*Harvella*) *elegans* Sowerby, Anderson, *Proc. Calif. Acad. Sci.*, Ser. 4, Vol. 18, No. 4, March 29, 1929, p. 176, pl. 21, figs. 5 and 6. Horizon M-N, of the Tuberá group, at the west foot of Tuberá Mountain, Colombia. Miocene.

[59] De Long, Jr., J. H., *Trans. San Diego Soc. Nat. Hist.*, Vol. 9, No. 25, April 30, 1941, p. 242. Also in table opposite p. 244 (as *Mactra "elegens"* Sowerby).

*Collecting Stations*: El Salvador: Meanguera Island, Gulf of Fonseca (199-D-1), 16 fathoms, sand, mud, crushed shell; Nicaragua: Monypenny Point, Gulf of Fonseca (199-D-5), 7 fathoms, mud.

*Description*: Shell elongately ovate, ventricose, thin, fragile, concentrically undulated; anterior end broadly rounded; posterior end very elongate, compressed, acutely rounded, gaping; beaks nearly medially or a little anteriorly situated; a narrow posterior dorsal area is bounded by a ridge at which the concentric undulations end abruptly; a depressed area in front of the beaks is not undulated; the undulations of the shell are ornamented with minute radial wrinkles. Large specimens almost entirely lack concentric undulations in the later stages of growth. The pallial sinus, tapering and sloping above, bluntly rounded at the end, extends about three-fifths the length of the shell and is free from the pallial line.

One of the larger specimens in the present collection measures approximately 45 mm. in length but it is not perfectly preserved. A large left valve in the collections of the California Academy of Sciences collected by Henry Hemphill at Scammon Lagoon, Lower California, measures: length, 119 mm.; height, 95 mm.; convexity (one valve), 36 mm.; pallial sinus projects anteriorly 89 mm. from the posterior margin of the shell.

Compared to the east American *Anatina* (*Raëta*) *canaliculata* Say, the west American shell is more elongate and tapering posteriorly and the beaks are more anteriorly situated.

The subspecies described as *Labiosa* (*Raëta*) *undulata gardnerae* Spieker, 1922, from the Miocene of Peru, and *Labiosa undulata mirandana* H. & K. Hodson, 1931, from the Miocene of Venezuela, are similar forms.

*Distribution*: A few valves of this fragile shell were dredged by the expedition in 7-16 fathoms in the Gulf of Fonseca. It is known to occur from Scammon Lagoon, Lower California, to northern Peru. It also has been recorded from the Miocene of Peru by Olsson[60] who placed in the synonymy of this species, *Raëta gibbosa* Gabb, described as a fossil from Peru, *Labiosa* (*Raëta*) *ventricosa* Spieker described from the Miocene of Peru, and *Labiosa* (*Raëta*) *hasletti* Anderson which was described from the Miocene of Colombia. *Anatina* (*Raëta*) *undulata* also has been recorded as occurring in the Miocene of Venezuela by H. & K. Hodson[61]. It also has been recorded as occurring in the Pliocene of Ecuador and Costa Rica and in the Pleistocene of Ecuador, Panama, Lower California and southern California.

## SUPERFAMILY MYACEA.

### FAMILY ALOIDIDAE.

Lamy[62] has recently published a revision of the Aloididae in the Museum of Natural History in Paris.

### Genus ***Aloidis*** Megerle von Mühlfeld.

*Corbula* Bruguière, Encycl. Méthod., 1797, pl. 230. [Species figured but not named].—Lamarck, Syst. Anim. s. Vert., 1801, p. 137. Species originally cited: *Corbula sulcata, C. laevigata, C. margaritacea, C. gallica, C. striata.*—Schmidt, Versuch. Conchyl. Samml., 1818, pp. 77, 177. "Typ. *Corbula sulcata*. Encyclop. Tab. 230. Fig. 1. a.b.c."

Not *Corbula* Bolten, Mus. Bolt., 1798, p. 184.—Winckworth, *Proc. Malacol. Soc. London,* Vol. 19, Pt. 1, March, 1930, p. 15. "I therefore designate *Corbula anomala*, Bolten, based on Chemnitz, 6, figs. 79, 80, as type of *Corbula*, which thus becomes an absolute synonym of *Asaphis*, Modeer, 1793."

*Aloidis* Megerle von Mühlfeld, Ges. Naturf. Freunde zu Berlin, Vol. 5, 1811, p. 67. Species cited: *Aloidis guineensis*. Ref. to "Linn. Syst. Nat. pag. 3287" and "Chemn. Conch. 10. t. 172. f. 1670. 1671."—Winckworth, *Proc. Malacol. Soc. London,* Vol. 19, Pt. 1, March, 1930, p. 15.

*Type* (by monotypy): *Aloidis guineensis* Megerle von Mühlfeld, based on Chemnitz, Neues Syst. Conchyl.-Cab., Bd. 10, 1788, pl. 172, figs. 1670 and 1671. "von der Guineischen Küste." (p.358). [=*Corbula sulcata* Lamarck. Illustrated by Vokes, *Bull. Amer. Mus. Nat. Hist.*, Vol. 86, Art. 1, 1945, pl. 1, figs. 1-5. Senegal. Recent].

The name *Aloidis* Megerle von Mühlfeld, 1811, replaces *Corbula* Bruguière, 1797, which was cited without named species. It also replaces *Corbula* of Lamarck, 1801, due to an earlier *Corbula* of Bolten, 1798, which has as type *Corbula anomala* Bolten. *Corbula* Bolten thus becomes a synonym of *Asaphis* Modeer. *Aloidis guineensis* Megerle von Mühlfeld, the type of *Aloidis*, is identical with *Corbula sulcata* Lamarck which is the type of *Corbula* Lamarck. *Aloidis* therefore exactly replaces *Corbula* as generally used in the literature. Vokes[63] has recently discussed this genus and considered *Corbula* Lamarck to be a valid name for it.

Species of *Aloidis* occur in many parts of the world in marine and brackish waters. They prefer the warmer waters and are said to occur especially abundantly in the China Sea.

About 18 species from west American waters have been described under the genus "*Corbula*".

---

60 *Labiosa* (*Raëta*) *undulata undulata* Gould, Olsson, *Bull. Amer. Paleo.*, Vol. 19, Bull. No. 68, June 30, 1932, p. 131, pl. 14, fig. 11. "Tumbez formation, Que. Tucillal at Zorritos." Peru. Miocene.

61 *Labiosa* (*Raeta*) *undulata* Gould, H. & K. Hodson, *Bull. Amer. Paleo.*, Vol. 16, No. 59, October 1, 1931, p. 21, pl. 7, fig. 6. Urumaco, District of Democracia, Falcón, Venezuela. Upper middle Miocene.

62 Lamy, E. Révision des Corbulidae vivants du Muséum National d'Histoire Naturelle de Paris. *Journ. de Conchyl.*, Vol. 84, No. 1, July 31, 1941, pp. 5-33, 6 figs. in text; Vol. 84, No. 2, November 15, 1941, pp. 121-144; Vol. 84, No. 3, December 2, 1941, pp. 211-254.

63 Vokes, H. E. Supraspecific Groups of the Pelecypod Family Corbulidae. *Bull. Amer. Mus. Nat. Hist.*, Vol. 86, Art. 1, October 10, 1945, pp. 7-10.

Key to the species of *Aloidis*.

A. Shell elongate, with a prominent, narrow rostrum
- a. Shell with a sharp, elevated carina posteriorly ............ *tenuis*[64]
- aa. Shell without an elevated carina posteriorly
  - b. With radial striae; white
    - c. Shell thick; fine striae on umbos ............ *nasuta*
    - cc. Shell thin; fine reticulate sculpture over entire shell.... *fragilis*
  - bb. Without radial striae; umbos and inner margins pink ............ *ovulata*

B. Shell trigonal or subquadrate
- a. Right valve much the larger; rayed with red ............ *speciosa*
- aa. Nearly equivalve, right valve slightly the larger
  - b. Posterior end obliquely truncated
    - c. Valves flattened; sculpture fine
      - d. Length exceeding 10 mm.; umbos purplish with two white radiating rays ............ *biradiata*
      - dd. Length usually not exceeding 10 mm.; white, yellow, bluish-gray, occasionally faintly biradiate ...... *luteola*
    - cc. Valves ventricose
      - e. Shell with red spot under beaks; often mottled ............ *marmorata*
      - ee. Shell entirely white
        - f. Posterior dorsal area with radial rows of pustules ........ *porcella*
        - ff. Posterior dorsal area without radial sculpture .......... *ventricosa*
  - bb. Posterior end abruptly truncated
    - g. Shell subglobose, nut-like form ............ *nuciformis*
    - gg. Shell subquadrate; posteriorly bicarinate ............ *bicarinata*

### Subgenus **Aloidis s.s.**

#### ***Aloidis (Aloidis) speciosa*** Reeve.

*Corbula radiata* Sowerby, *Proc. Zool. Soc. London*, May 17, 1833, p. 36, "Hab. ad Acapulcam." "A single specimen was picked up on the sands."

Not *Corbula radiata* Brocchi, 1814. Fossil in Italy.

*Corbula speciosa* Reeve, Conch. Icon., Vol. 2, *Corbula*, August, 1843, species 6, pl. 1, fig. 6. "Hab. Gulf of Nicoya (dredged in seven fathoms' water)."—Hinds, *Proc. Zool. Soc. London*, November, 1843, p. 57. "Hab. Panama; from six fathoms, mud. Gulf of Nicoya, Central America."—Hinds, Zool. Voy. Sulphur, Moll., Pt. 3, 1844 [January, 1845, on cover of Pt. 3], p. 68, pl. 20, figs. 7, 8. Original locality cited.

*Type Locality*: Gulf of Nicoya, Central America, in 7 fathoms.

*Range*: Santa Inez Bay, Gulf of California, to Panama Bay.

*Collecting Stations*: Mexico: Santa Inez Bay, Gulf of California (142-D-2), 30-35 fathoms, muddy sand, crushed shell; 13 miles west of Mazatlan (155-D-1), 56 fathoms, mud; 3 miles off Pyramid Rock, Clarion Island (163-D-2), 55 fathoms, rock, coral; Nicaragua: Corinto (200-D-19), 12-13 fathoms, mangrove leaves; Costa Rica: 14 miles S. × E. of Judas Point (214-D-1-4), 42-61 fathoms, mud, rocks.

*Description*: Shell trigonally ovate, very inequivalve, high, thick, rounded anteriorly, posteriorly somewhat rostrate, truncated at the end, the posterior area set off by a strong angulation; escutcheon and lunular areas present; right valve the larger, with deeply grooved concentric rugose sculpture; the left valve finely, somewhat obliquely, concentrically grooved; umbonal area of each valve with radial striae on perfect specimens; both valves whitish rayed with bright red or occasionally mostly red.

A specimen dredged off Clarion Island, measures: length, 19.2 mm.; height, 15.4 mm.; convexity (both valves together), 12.5 mm.

The shells of fully grown individuals of *Aloidis speciosa* are ornamented with deep red colored rays which are unusually bright and well defined for a member of this genus. A considerable number of smaller shells having the same shape as young stages of the full grown colored forms have been referred to *A. speciosa* but they do not possess a trace of the vivid coloration. These are subrectangular, only moderately inequivalve with a sharp posterior umbonal angulation, slightly depressed medially, and perfect specimens are ornamented by fairly widely spaced concentric ribbing which together with the interspaces is crossed by fine radial striae. Such young specimens might easily be mistaken for some other species.

*Aloidis dietziana* C. B. Adams[65] is a similar species occurring in the Caribbean region.

*Distribution*: *Aloidis speciosa* was dredged by the expedition at a few localities from the Gulf of California to Costa Rica, in 30-61 fathoms. It is recorded here for the first time from Clarion Island and from the Gulf of California although it was known to occur at the Tres Marias Islands and south to Panama.

### Subgenus **Caryocorbula** Gardner.

*Caryocorbula* Gardner, *Nautilus*, Vol. 40, No. 2, October, 1926, p. 46. "Type.—*Corbula alabamiensis* Isaac Lea. Claiborne Eocene of

---

[64] Not represented in the present collection.

[65] *Corbula dietziana* C. B. Adams, *Contrib. to Conch.*, No. 12, October, 1852, p. 235. "Habitat.—Kingston harbor (Jamaica), along the 'Palisades,' southeast from the city." —Dall, *Bull. Mus. Comp. Zool.*, Vol. 12, No. 6, September, 1886, p. 314, pl. 1, figs. 5, 5a, 5b. "Identified and figured from the types."

the East Coast and Gulf from South Carolina to the Rio Grande."—Gardner, *U. S. Geol. Surv., Prof. Paper* 142-E, 1928, p. 230. "Type: *Corbula alabamiensis* Isaac Lea."

*Type* (by original designation): *Corbula alabamiensis* Lea [*Contrib. Geol.*, December, 1833, p. 45, pl. 1, fig. 12. Tertiary of Claiborne, Alabama].

Shell small or of moderate dimensions; acutely keeled posteriorly; slightly inequivalvate; the right valve a little larger and a little higher relatively than the left; both valves concentrically rugose, the sculpture upon the right valve in some species stronger and more regular than upon the left; a microscopically fine radial lineation developed in some of the later species, particularly upon the posterior keel; ligament, dental muscle and sinal characters similar to those of *Corbula s.s.* (Gardner).

**Aloidis (Caryocorbula) bicarinata** Sowerby.

*Corbula bicarinata* Sowerby, *Proc. Zool. Soc. London*, May 17, 1833, p. 35. "Hab. ad littora Columbiae Occidentalis." "Found in sandy mud at from seven to seventeen fathoms at Panama, Real Llejos, Caraccas and St. Elena."—Hanley, Cat. Rec. Bivalve Shells, 1843, p. 46, suppl. pl. 12, fig. 31. "W. Columbia."—Reeve, Conch. Icon., Vol. 2, *Corbula*, January, 1844, species 23, pl. 3, fig. 23. Original localities cited.

*Type Locality*: Panama, in 17 fathoms (here designated as type locality). Real Llejos, Caraccas and Santa Elena also cited originally.

*Range*: Gulf of California to Guayaquil, Ecuador (Dall).

*Collecting Stations*: Guatemala: 7 miles west of Champerico (197-D-2), 14 fathoms, mud; El Salvador: La Union, Gulf of Fonseca (199-D-22), 3 fathoms, mud, mangrove leaves; Nicaragua: Corinto (200-D-19), 12-13 fathoms, mangrove leaves, also on beach.

*Description*: Shell squarely ovate, nearly equilateral and equivalve, moderately thick, whitish, anteriorly rounded, posteriorly abruptly truncated; a sharp umbonal angulation runs from the beaks to the posterior ventral margin and another angulation occurs between this and the dorsal margin; a depressed area occurs below the beaks and a rather smooth, depressed, elongately ovate escutcheon occurs back of the beaks; both valves are sculptured with fine, nearly evenly spaced, concentric threads.

The specimens in the present collection are somewhat worn. A well preserved specimen from Guaymas Bay, Mexico, in the collections of the California Academy of Sciences, measures: length, 11.8 mm.; height, 8.5 mm.; convexity (both valves together), 7.2 mm.

*Corbula alba* Philippi[66] was described from Mazatlan, Mexico. It was said to resemble "*Corbula*" *bicarinata* and Carpenter[67] suggested that it might be referable to the species described by Sowerby.

[66] *Corbula alba* Philippi, *Zeit. f. Malakozool.*, Jahrg. 3, January, 1846, p. 19. "Patria: Mazatlan."

[67] Carpenter, P. P., *Rept. Brit. Assoc. Adv. Sci.* for 1856 (issued 1857), p. 224.

*Distribution*: This species was dredged by the expedition from Guatemala to Nicaragua in 12-14 fathoms and was taken in the beach drift at Corinto, Nicaragua.

**Aloidis (Caryocorbula) biradiata** Sowerby.

*Corbula biradiata* Sowerby, *Proc. Zool. Soc. London*, May 17, 1833, p. 35. "Hab. ad Chiriqui et ad sinum caraccensem." "Found in mud and sand in from three to six fathoms at Chiriqui, and in seven fathoms in the Bay of Caraccas."—Reeve, Conch. Icon., Vol. 2, *Corbula*, August, 1843, species 3, pl. 1, fig. 3. Original localities cited.—Hanley, Cat. Rec. Bivalve Shells, 1843, p. 47, suppl. pl. 10, fig. 51. Caraccas, Ecuador.

*Corbula rubra* C. B. Adams, *Ann. Lyceum Nat. Hist. New York*, Vol. 5, July, 1852, pp. 523, 548 (separate pp. 299, 324). "Habitat.—Panama."—Carpenter, *Proc. Zool. Soc. London*, 1863, p. 368. Reprint in *Smithson. Miscell. Coll.*, No. 252, 1872, p. 204. "A young orange-tinted specimen of *C. biradiata*, No. 503. The broad 'flexure' is an accidental growth, not shown in the lines of growth of an earlier stage."

*Corbula polychroma* Carpenter, *Proc. Zool. Soc. London* for 1856, p. 198 (issued January 7, 1857). "Hab. In Sinu Californiensi (Lieut. Shipley in Mus. Cuming.)." [Not the record "Sta. Barbara (Col. Jewett in Mus. Gould)." = *C. luteola* Carpenter].

*Type Locality*: Chiriqui, Panama, in 3-6 fathoms mud and sand (here designated as type locality). Bay of Caraccas, Ecuador, also cited originally.

*Range*: Guaymas, Mexico, to Guayaquil, Ecuador.

*Collecting Stations*: El Salvador: La Union (199-D-22), 3 fathoms, mud, mangrove leaves; Nicaragua: Corinto (200-D-4-7, 17, 19), ½-13 fathoms, mangrove leaves, sand, also in beach drift; Costa Rica: Port Parker, on beach.

*Description*: Shell ovately oblong, somewhat compressed, nearly equivalve, the right valve slightly the larger; anterior end rounded; posterior end somewhat projecting, the end obliquely truncated, a sharp umbonal angulation is present; an area in front of the beaks is depressed, likewise an elongately ovate sloping area back of the beaks; valves sculptured with fine, fairly close concentric striae; color light purple with two white radiating rays, one along each umbonal ridge, the interior often blood red.

A well preserved specimen in the collections of the California Academy of Sciences which was collected by the senior author on the beach at Panama City, measures: length, 13.5 mm.; height, 9 mm.; convexity (both valves together), 6.2 mm.

Perfect specimens of this species may be recognized by the two radiating white rays and often by the blood red color of the interior.

*Distribution*: Specimens of this species were taken by the expedition from the Gulf of Fonseca to Port Parker, Costa Rica, at

depths of ½ to 13 fathoms, as well as on the beach. It has been cited by Pilsbry & Olsson as occurring in the Pliocene of Ecuador and in the Pleistocene of Panama by Olsson. Rutten[68] cited "*Corbula* cf. *biradiata*" from the Quaternary of Surinam in the Dutch West Indies but probably that record can be referred to a Caribbean species.

### *Aloidis (Caryocorbula) luteola* Carpenter.

*Corbula luteola* Carpenter, *Rept. Brit. Assoc. Adv. Sci.* for 1863 (issued August, 1864), pp. 611, 637. From the region between San Diego and San Pedro, California. Reprint in *Smithson. Miscell. Coll.*, No. 252, 1872, pp. 97, 123—Carpenter, *Proc. Calif. Acad. Nat. Sci.*, Vol. 3, February, 1865, p. 207. "Hab. San Diego, San Pedro, 50, alive, at low water."—Arnold, *Mem. Calif. Acad. Sci.*, Vol. 3, 1903, p. 181, pl. 17, fig. 11. Pliocene of San Pedro, Pleistocene of San Pedro, Los Cerritos and San Diego, California, and Recent in the same region.

*Corbula (Lentidium) luteola* Carpenter, Grant & Gale, *Mem. San Diego Soc. Nat. Hist.*, Vol. 1, 1931, p. 421, pl. 19, figs. 2 and 7. Upper Miocene of California and Pleistocene of California and Lower California. Recent from Monterey, California, to Acapulco, Mexico (Jordan).

*Type Locality*: Between San Diego and San Pedro, California.

*Range*: Monterey, California, to Cape San Lucas, Lower California.

*Collecting Station*: Mexico: Cape San Lucas, Lower California, on beach.

*Description*: Shell similar to *C. biradiata*, but much smaller; not obese, transverse, rosy-yellow, toward the dorsal area sometimes obscurely biradiate; angle much less carinate, posteriorly defined; anterior rounded, expanded; concentrically closely but obtusely lirate; umbos obtuse; interior with small teeth; pallial line angulate, not sinuated; adductor scars thick; margin in adult shell overlapping posteriorly. Length, 0.42; height, 0.28; diameter, 0.16. (Free translation of Carpenter's description, 1865).

A specimen of this species in the collections of the California Academy of Sciences collected at San Diego, California, by O. N. Sanford, measures: length, 10 mm.; height, 6.8 mm.; convexity (both valves together), 4.6 mm.

Some of the characteristic features of this little nearly equivalve shell are the rather compressed form, subcentral beaks which are only slightly anteriorly situated and the fine, close, concentric sculpture.

*Aloidis luteola rosea* Williamson, 1905, is a rose colored form of this species.

*Aloidis luteola* is very similar to *Aloidis biradiata* as mentioned by Carpenter but it is smaller and usually less colored on the umbonal region.

Verco called attention to the compressed form of *Corbula compressa*,[69] an Australian species, and its similarity to *Aloidis luteola* in this feature. They are of course quite distinct species. The species described by Verco was later renamed *Corbula verconis* by Finlay.

*Distribution*: A few somewhat worn valves referable to this species were taken by the expedition on the beach at Cape San Lucas, Lower California. E. K. Jordan cited the species as ranging south to Acapulco, Mexico, but we have not seen specimens from south of Cape San Lucas. According to Burch this species is often found on a bottom of rocky rubble. It also has been reported as occurring from upper Miocene to Recent in California and in the Pleistocene of Lower California.

### *Aloidis (Caryocorbula) marmorata* Hinds.

Plate II, Fig. 17.

*Corbula marmorata* Hinds, *Proc. Zool. Soc. London*, November, 1843, p. 58. "Hab. West coast of Veragua; from twenty-six fathoms, mud." "Cab. Belcher."—Hinds Zool. Voy. Sulphur, Moll., Pt. 3, January, 1845 (on cover), p. 69, pl. 20, fig. 13. Original locality cited.—Reeve, Conch. Icon., Vol. 2, *Corbula*, May, 1844, species 39, pl. 5, fig. 39. Original locality cited.

*Type Locality*: West coast of Veragua, Panama, in 26 fathoms, mud.

*Range*: Punta Penasco, Sonora, Mexico, to Panama.

*Collecting Stations*: Mexico: Port Guatulco (195-D-9), 7 fathoms, gr. sand, crushed shell; Nicaragua: Corinto, beach; Costa Rica: Port Parker (203-D-1, 3), 12-15 fathoms, sandy mud, shelly mud, crushed shell.

*Description*: Shell small, ovately trigonal, nearly equivalve, whitish, mottled, a purplish-red spot present under the beaks; rounded in front, slightly projecting posteriorly and obliquely truncated at the end, often with a short lamellated projection; a strong posterior umbonal angulation marks off a flattish sloping posterior area; an excavated area is present beneath the beaks but only a minute sloping escutcheon is present back of the beaks; sculpture consists of strong, often somewhat angular or carinate concentric ribs which continue with equal strength over the posterior area but become finer toward the posterior and anterior dorsal margins; the interspaces and especially the posterior dorsal area is ornamented with fine radial striae; interior often pinkish with well defined whitish adductor impressions.

One of the largest specimens in the present collection measures: length, 7 mm.; height, 4.8 mm.; convexity (both valves together), 3.4 mm.

The shell of this species is characterized by the presence of a purplish-red spot under

[68] Rutten, L. M. R., *Leidische Geol. Mededeel.*, Deel 5, 1931, p. 661.

[69] *Corbula compressa* Verco, *Trans. Roy. Soc. South Australia*, Vol. 20, Pt. 2, December, 1896, p. 230, pl. 8, figs. 2, 2a, 2b. "Habitat.—Yankalilla Bay, in sludge, at 20 fathoms, many alive; Backstairs Passage, Port Lincoln, Eastern Cove, Kangaroo Island, at varying depths, several (Verco)."

*Corbula verconis* Finlay, *Trans. New Zealand Inst.*, Vol. 57, 1927, p. 531. New name for *Corbula compressa* Verco, 1896, not *C. compressa* Lea, 1833.

the beaks and by the strong concentric and fine radial sculpture.

*Corbula venusta* Angas,[70] an Australian species, ornamented with a short carnelian-red ray at the anterior side of the umbos, was compared by its author to *Aloidis marmorata*.

*Distribution*: This species was taken by the expedition from Port Guatulco, Mexico, to Costa Rica, on the beach and at depths of 7-15 fathoms.

### *Aloidis (Caryocorbula) nasuta* Sowerby.

Plate II, Fig. 9.

*Corbula nasuta* Sowerby, *Proc. Zool. Soc. London*, May 17, 1833, p. 35. "Hab. ad Xipixapi." "Found in sandy mud at a depth of ten fathoms. Some small specimens which I suppose to be the young of this species were found in the gulf of Nicoiyo."—Reeve, Conch. Icon., Vol. 2, *Corbula*, August, 1843, species 1, pl. 1, fig. 1. Original locality records cited.

*Corbula pustulosa* Carpenter, Cat. Mazatlan Shells, August, 1855, p. 22. "Panama and St. Blas, 33 fm. R. B. Hinds, Mus. Cuming. —Mazatlan: one small pair nestling in *Spondylus*, and 1 valve in *Chamae*, L'pool Col."

*Type Locality*: Xipixapi [Jipijapa], Ecuador, in 10 fathoms, sandy mud. (Of *Corbula pustulosa* Carpenter, Panama, in 33 fathoms, here selected as type locality).

*Range*: Magdalena Bay, Lower California, to Punta Penasco, Sonora, Mexico, in the Gulf of California, and south to Zorritos, Peru.

*Collecting Stations*: Mexico: Santa Inez Bay, Gulf of California (145-D-1-3), 4-13 fathoms, sand; Cape San Lucas; 4 miles SSW. of Maldonado Point (192-D-3), 38 fathoms, mud; Port Guatulco (195-D-20), 23 fathoms, mud; Tangola-Tangola Bay (196-D-14, 15, 19, 20), 5-50 fathoms, crushed shell, mud; Guatemala: 7 miles west of Champerico (197-D-1, 2), 14 fathoms, mud; El Salvador: La Libertad (198-D-1, 2), 13-14 fathoms, mud; Meanguera Island, Gulf of Fonseca (199-D-1), 16 fathoms, sand, mud, crushed shell; La Union, Gulf of Fonseca (199-D-12, 13), 5-6 fathoms, mud; Nicaragua: Corinto (200-D-16, 19), 4-13 fathoms, mangrove leaves, also on beach; Costa Rica: Port Parker (203-D-1, 3), 12-15 fathoms, shelly sand, crushed shell, shelly mud; Cedro Island, Gulf of Nicoya (213-D-1-10), 4-10 fathoms, mud, sand, crushed shell; Golfito (218), 16 fathoms, sand, mud, crushed shell.

*Description*: Shell elongately oval, inflated, inequivalve, the right valve the larger, thick, white, rostrate posteriorly; posterior umbonal angulation present, the posterior dorsal area is somewhat excavated; a depressed elongate escutcheon is set off by an angulation; sculpture consists of moderately fine but somewhat irregular concentric threads sometimes coarser toward the ventral margin, and on the early part of the shell fine radial striae composed of very fine pustules.

A large but somewhat worn right valve from Corinto, Nicaragua, in the present collection measures: length, 14 mm.; height, 9 mm.; convexity (one valve), 4.4 mm. The posterior attenuation at the end of the valve is, as often happens, worn off. A smaller perfect specimen in the collection of the California Academy of Sciences, dredged off Mexico, measures: length, 13 mm.; height, 7 mm.; convexity (both valves together), 6.5 mm.

As mentioned long ago by Mörch and more recently by Olsson, the umbonal area of this species is ornamented with fine radial striae. These striae are composed of very fine pustules. Hundreds of small shells in the present collection with this type of radial sculpture agree exactly with Carpenter's description of *Corbula pustulosa*. These appear to be identical with the young stages of *Aloidis nasuta*. We have therefore placed Carpenter's species in the synonymy of *Aloidis nasuta*.

Reeve's figure[71] of *"Corbula" obesa* Hinds is of a small, elongate shell somewhat similar to that of young *Aloidis nasuta*. Hind's original illustration of *"Corbula" obesa* indicates a higher, more globose shell similar to that of *A. porcella* Dall. In view of the fact that no radial striae were mentioned by Reeve we have hesitated to refer his illustration of *"Corbula" obesa* to *A. nasuta* but it seems quite possible that it may be referable to Sowerby's species.

*Aloidis nasuta* has been recorded in the literature as occurring in distant localities, but so far as known it occurs only in west American waters. Hedley[72] mentioned that it was erroneously recorded from Sydney, Australia. Von Ihering[73] cited it from Brazil. The species described by Conrad[74] as *Corbula nasuta* from the Eocene of Alabama, was later referred by Dall to *"Corbula" alabamiensis* Lea. The species cited as *Corbula nasuta* by Conrad,[75] from the Tertiary of Texas was later considered to be a distinct species and was named *Corbula conradi* by Dall.[76] That species, at the present time, is known to occur in the Caribbean region from Cape Hatteras to Cartagena Bay, Colombia, in 4 to 63 fathoms.

*"Corbula" nelsoni* Olsson, 1932, described

---

[70] *Corbula venusta* Angas, *Proc. Zool. Soc. London*, January 3, 1871, p. 20, pl. 1, fig. 29. "Hab. Dredged on the 'Sow and Pigs' bank, Port Jackson." Australia.

[71] *Corbula obesa* Hinds, Reeve, Conch. Icon., Vol. 2, *Corbula*, May, 1844, species 38, pl. 5, fig. 38. Cited from Veragua, Panama, and San Blas, Mexico, in 20-32 fathoms.

[72] Hedley, C., *Jour. Roy. Soc. New South Wales*, Vol. 51, Suppl., 1918, p. M31.

The species referred to *Corbula nasuta* in Australia is probably *C. coxi* Pilsbry, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 49, 1897, p. 363, pl. 9, figs. 1, 2, 3. "Sydney Head (John Brazier), and Eden, Twofold Bay, New South Wales (Dr. J. C. Cox)."

[73] Von Ihering, H., *Rev. Mus. Paulista*, Vol. 2, 1897, p. 169.

[74] *Corbula nasuta* Conrad, Foss. Shells Tert. Form., Vol. 1, No. 3, August, 1833, p. 60 (38), pl. 19, fig. 4. "Locality, Claiborne, Alab."

[75] *Corbula nasuta* Conrad, Conrad, Rept. Mexican Boundary Survey, Vol. 1, Pt. 2, 1857, p. 161, pl. 19, fig. 4. "Locality.—Western Texas." Tertiary.

[76] Dall, W. H., *Trans. Wagner Free Inst. Sci.*, Vol. 3, Pt. 4, April, 1898, p. 842. Illustrated by Dall, *U. S. Nat. Mus., Bull.* 37, 1889, pl. 2, figs. 6a, 6b, 6c, 6d. See Maury, *Bull. Amer. Paleo.*, Vol. 8, Bull. No. 34, 1920, p. 140 (108).

from the Miocene of Peru, is similar to *Aloidis nasuta.*

*Distribution*: Specimens of *Aloidis nasuta* were taken by the expedition from Santa Inez Bay in the Gulf of California to the Gulf of Dulce in Costa Rica, on the beach and dredged at depths of 4 to 50 fathoms. It occurs in this region more commonly than any other species of *Aloidis* and ranges south to Zorritos, Peru. It also has been recorded as occurring in the Pliocene of Ecuador.

**Aloidis (Caryocorbula) nuciformis** Sowerby.

Plate II, Fig. 1.

*Corbula nuciformis* Sowerby, *Proc. Zool. Soc. London,* May 17, 1833, p. 35. "Hab. in Americâ Centrali." "Found at a depth of six fathoms in sandy mud at Real Llejos." Also found as a fossil near Guayaquil, Ecuador. —Reeve, Conch. Icon., Vol. 2, *Corbula*, September, 1843, species 9, pl. 2, fig. 9. Original locality cited.

*Type Locality*: Real Llejos [near Corinto], Nicaragua, in 6 fathoms, sandy mud.

*Range*: Concepcion Bay, Gulf of California, to Guayaquil, Ecuador.

*Collecting Stations*: Mexico: Tangola-Tangola Bay (196-D-20), 50 fathoms, mud; Costa Rica: off Ballena Bay, Gulf of Nicoya (213-D-11-17), 35-40 fathoms, mud.

*Description*: Shell trigonally ovate, very inflated, nearly equivalve, right valve a little the larger, beaks nearly central, white covered by a brownish periostracum, anteriorly rounded, posteriorly shortly rostrate and truncated at the end; a depressed radial area present anterior to the posterior umbonal angulation; along the posterior dorsal margin a depressed area is set off by an angulation; exteriorly the valves are concentrically grooved which results in fine, rounded, somewhat irregular concentric riblets.

One of the largest specimens in the present collection measures: length, 11.5 mm.; height, 9.8 mm.; convexity (both valves together), 8 mm. Another specimen measures: length, 10.4 mm.; height, 9.8 mm.; convexity (both valves together), 8.2 mm.

As suggested by its specific name, the shell of this species is characterized by the subglobose, rounded, nut-like form. The posterior rostration is very short and abruptly truncated in comparison to *A. nasuta.*

*Distribution*: This species was dredged by the expedition at two localities, off Tangola-Tangola Bay, Mexico, and off Ballena Bay, Costa Rica, in 35-50 fathoms, on a mud bottom. At the time of the original description of this species Sowerby mentioned that it also occurs as a fossil near Guayaquil, Ecuador.

**Aloidis (Caryocorbula) ovulata** Sowerby.

Plate II, Fig. 11.

*Corbula ovulata* Sowerby, *Proc. Zool. Soc. London,* May 17, 1833, p. 35. "Hab. ad littora Americae Meridionalis." "Found in sandy mud at various depths, from seven to seventeen fathoms, at Xipixapi, and in the Bays of Montijo and Caraccas. Detached valves of a beautiful pink colour were picked up on the sands at Real Llejos and Mazatlan."—Reeve, Conch. Icon., Vol. 2, *Corbula*, August, 1843, species 7, pl. 1, fig. 7. Original locality records cited.—Hanley, Cat. Rec. Bivalve Shells, 1843, p. 47, suppl. pl. 10, fig. 52. South America.

*Corbula* cf. *collazica* Maury, Li, *Bull. Geol. Soc. China*, Vol. 9, No. 3, October, 1930, p. 263, pl. 5, figs. 36, 36a (on expl. to plate as *C. collazia*). Dredged in Panama Bay, in 10-40 feet. "Horizon: Gatun formation."—Pilsbry, *Proc. Acad. Nat. Sci. Philadelphia,* Vol. 83, 1931, p. 431. "=*Corbula ovulata* Sowb." Recent.

*Type Locality*: Xipixapi [Jipijapa], Ecuador (here designated as type locality). Bay of Caraccas, Ecuador, and Montijo Bay, Panama, also cited originally.

*Range*: Ballandra Bay in the Gulf of California to Punta Picos, Peru.

*Collecting Stations*: Mexico: Banderas Bay, beach; Chamela Bay, beach; Tenacatita Bay, beach; Manzanillo (184-D-2), 30 fathoms, gravelly sand; Guatemala: 7 miles west of Champerico (197-D-2), 14 fathoms, mud; El Salvador: La Libertad (198-D-2), 14 fathoms, mud; Nicaragua: Corinto (200-D-20-26), 1.5-6.5 fathoms, mangrove leaves, also on beach; Isla Cardon; Costa Rica: Culebra Bay, beach.

*Description*: Shell elongately ovate, nearly equivalve, thick, rounded anteriorly, rostrate posteriorly, posterior umbonal ridge present; posterior dorsal area sloping, flattened or slightly excavated; along the dorsal margin a long sloping area is marked off by a carination; valves finely concentrically grooved; color purplish or pink on umbonal area and beaks, distal areas white; interior white, tinged with pink around the margins.

A specimen in the collections of the California Academy of Sciences dredged near Acapulco, Mexico, by the Templeton Crocker Expedition, 1932, measures: length, 24 mm.; height, 14 mm.; Convexity (both valves together), 11.5 mm.

The large size, elongately ovate shape, and purplish-pink color of the umbonal areas and inner margins are characteristic features of this species.

The inner surface of the posterior end of some specimens shows two depressions corresponding to siphonal tubes such as mentioned by Vokes[77] in some Cretaceous and Eocene species of Aloididae.

*Distribution*: This species was taken by the expedition at a number of localities from Banderas Bay, Mexico, to Culebra Bay, Costa Rica, on beaches and at depths of 1.5 to 30 fathoms. It also has been recorded as occurring in the Miocene of Peru by Olsson[78], the Pliocene of Panama and Costa Rica, and in the Pliocene of Ecuador by Pilsbry & Olsson.

[77] Vokes, H. E., *Amer. Jour. Sci.*, Vol. 242, No. 11, November 1, 1944, p. 619.

[78] *Corbula (Caryocorbula) ovulata* Sowerby, Olsson, *Bull. Amer. Paleo.*, Vol. 19, Bull. 68, June 30, 1932, p. 140. "Tumbez formation, Que. Tucillal at Zorritos."

**Aloidis (Caryocorbula) porcella** Dall.

Plate II, Figs. 13 & 15.

*Corbula porcella* Dall, *Proc. U. S. Nat. Mus.*, Vol. 52, No. 2183, December 27, 1916, p. 415. "Station 2838, off Lower California, in 44 fathoms, mud. The species extends northward to the Santa Barbara Islands, California." [Station 2838=Lat. 28° 12′ 00″ N., Long. 115° 19′ 00″ W., in 44 fathoms, green mud].—Dall, *U. S. Nat. Mus., Bull.* 112, 1921, p. 54. Santa Rosa Island, California, to Panama.—I. S. Oldroyd, *Stanford Univ. Publ. Univ. Ser. Geol. Sci.*, Vol. 1, 1924, p. 204. Same records as cited by Dall.

*Type Locality*: East of Cedros Island, Lat. 28° 12′ 00° N., Long. 115° 09′ 00″ W., off Lower California, in 44 fathoms, green mud.

*Range*: Santa Rosa Island, California, to Panama (Dall).

*Collecting Stations*: Mexico: East of Cedros Island (126-D-9, 12, 15), 42-56 fathoms, crushed shell, mud; Costa Rica: off Ballena Bay, Gulf of Nicoya (213-D-11-17), 35-40 fathoms, mud.

*Description*: Shell small, ashy white, inequivalve, the left valve smaller; inequilateral, the posterior end larger; rounded in front, pointed behind; a prominent angle separates the posterior dorsal area from the rest of the disk; surface concentrically evenly threaded, the threads a little more pronounced on the dorsal area; an obscure almost microscopic radial striation is sometimes apparent; the siphons protrude beyond the rostrum with a dense covering of wrinkled periostracum; interior white, hinge normal, the basal margin of the right valve partly overlapping that of the left valve; pallial sinus obsolete. Length, 8.5; height, 4; diameter, 4.5 mm.; but the shell is often larger. (Original description).

Specimens in the present collection from near the type locality of *Aloidis porcella* agree with Dall's description of that species. There is variation in size; a large specimen measures: length, 7.8 mm.; height, 5.1 mm.; convexity (both valves together), 4.4 mm.

This species is characterized by the rather high, trigonal, convex valves on which the beaks are anteriorly situated, and by the radial striae composed of rows of pustules on the posterior dorsal area as well as, sometimes, on the umbonal area. The pustules, when present on the umbonal area are well developed and rather widely spaced. These features as well as the coarser concentric sculpture easily separate the species from *Aloidis luteola*. The more highly trigonal shell, the shorter posterior end and wider posterior dorsal area are features which serve to separate *A. porcella* from the young of *A. nasuta*. The radial sculpture of *A. porcella* is composed of coarser and more widely spaced pustules than that of the young of *A. nasuta*.

The original illustration of "*Corbula*" *obesa* Hinds[79] represents a small shell similar to the ones here referred to *Aloidis porcella*. No mention was made of radial sculpture in Hind's original description. This character on *A. porcella* is sometimes only faintly developed. Dall, 1921, cited both *A. porcella* and *A. obesa* as ranging from southern Californa to Panama. It seems possible that the two may be identical or that the species described by Dall may be only a subspecies of *A. obesa*. However, until it is known whether or not radial sculpture is present on Hind's type of *A. obesa* we have considered it advisable to recognize Dall's species as valid. It has already been mentioned under the discussion of *Aloidis nasuta* Sowerby that the shell illustrated by Reeve under the name "*Corbula*" *obesa* is elongate in outline and bears a resemblance to Sowerby's species, *A. nasuta*, rather than to *A. obesa*.

*Distribution*: This species was dredged by the expedition at three localities near the type locality, east of Cedros Island, off Lower California, in 42-56 fathoms, on a bottom of crushed shell and mud, also in Ballena Bay, Costa Rica, in 35-40 fathoms. It also has been recorded as occurring in the Pleistocene of Magdalena Bay, Lower California. The species cited under the name of "*Corbula fragilis*" from the Pleistocene of Tomales Bay, California, appears to be referable to *Aloidis porcella* or a similar species.

**Aloidis (Caryocorbula) ventricosa** Adams & Reeve

Plate II, Figs. 3 & 4.

*Corbula ventricosa* A. Adams & Reeve, Zool. Voy. Samarang, Moll., August, 1850, p. 83, pl. 23, fig. 12. "Hab. China Sea."—Carpenter, *Rept. Brit. Assoc. Adv. Sci.* for 1856 (issued 1857), pp. 284, 300. Bay of Panama; Gulf of California.

*Type Locality*: "China Sea" originally cited but this is now believed to be erroneous. Typical specimens have been collected near Acapulco, Mexico.

*Range*: Gulf of California to Panama.

*Collecting Station*: Mexico: Tangola-Tangola Bay (196-D-20), 50 fathoms, mud.

*Description*: Shell subtrigonally-ovate, ventricose, anteriorly rounded, posterior a little the longer, angulated, subtruncated, dirty white, partly covered with a dusky periostracum. (Free translation of original description). "A very dull simple species, peculiar in form." (Adams & Reeve).

In addition to the foregoing description it can be remarked that the shell is somewhat variable. The right valve is a little the larger; a strong posterior umbonal angulation and sometimes anterior to this a low radial depression is present; toward the dorsal margin another but weaker angulation is pres-

[79] *Corbula obesa* Hinds, *Proc. Zool. Soc. London*, November, 1843, p. 57. "Hab. The west coast of America, between 8° 57′ and 21° 32′ north latitude, in from twenty-two to thirty-three fathoms, mud; namely, Panama, coast of Veragua, and San Blas."—Hinds, Zool. Voy. Sulphur, Moll., Pt. 3, 1844 [January, 1845 on cover], p. 68, pl. 20, fig. 12. Original locality cited.

ent and between this and the first angulation and also between it and the dorsal margin the shell is sometimes slightly excavated; lunular region excavated but not circumscribed; sculptured with strong somewhat irregular, concentric grooves; exteriorly dirty white partly covered by a dull olive periostracum, the interior white.

The largest specimen in the present collection measures: length, 13.6 mm.; height, 9.8 mm.; convexity (both valves together), 8.2 mm.

A few specimens dredged by the expedition off Tangola-Tangola Bay, west Mexico, are identical with shells in the collections of the California Academy of Sciences which were dredged off west Mexico by the Templeton Crocker expedition in 1932. Carpenter in 1857 cited *"Corbula" ventricosa* Adams & Reeve from Panama and the Gulf of California. The original locality for that species given by Adams & Reeve was "China Sea." We have not noticed any citation of that species in recent lists of mollusks found in that general region. It has already been pointed out in the discussion of *Taras sericata* Reeve that several species collected by Belcher and described by Adams & Reeve which were said to come from Oriental waters are now known to occur only in west American waters where Belcher collected during a former expedition. These include the species cited by Adams & Reeve as *Lucina sericata*, *Artemis dunkeri*, *Cytherea virginea* and *Mactra thracioides*. These occurrences serve to strengthen the reliability of Carpenter's record of *"Corbula" ventricosa* from west American waters, especially when it is realized that Carpenter had access to the types in the British Museum for comparative purposes. These facts together with the fact that our specimens agree well with the original description and illustration of *"Corbula" ventricosa* have led us, at least for the present, to identify our shells with the species described by Adams & Reeve.

The species described as *Corbula* (*Cuneocorbula*) *ira* by Dall[80], from the Gulf of Panama in 182 fathoms, appears to be a similar species. The type was not illustrated. Dall compared his species to *"Corbula" knoxiana* Adams[81] from Jamaica which species, he stated, was more elongated and has three instead of two ridges on the dorsal area. The right valve of Dall's species was said to be the smaller while in the present shell the right valve is a little the larger and overlaps the left. The concentric sculpture on Dall's species appears to be more regular and a little more widely spaced. These differences appear to separate the present specimens from Dall's species but the lack of illustration of Dall's type precludes any further opinion as to the relationship of the two.

---

[80] *Corbula* (*Cuneocorbula*) *ira* Dall, *Bull. Mus. Comp. Zool.*, Vol. 43, No. 6, October, 1908, p. 423. "U.S.S. 'Albatross,' station 3355, Gulf of Panama, in 182 fathoms, mud, bottom temperature 54.1° F. U.S.N.M. 122,944."

[81] See Dall, W. H., *Bull. Mus. Comp. Zool.*, Vol. 12, No. 6, September, 1886, p. 313, pl. 1, figs. 3, 3a, 3b, 3c. Figures of Adams' type.

*Distribution*: This species was dredged by the expedition at Tangola-Tangola Bay, Mexico, in 50 fathoms on a muddy bottom. It also was dredged near Acapulco, Mexico, by the Templeton Crocker Expedition in 1932.

### Subgenus **Tenuicorbula** Olsson.

*Tenuicorbula* Olsson, *Bull. Amer. Paleo.*, Vol. 19, Bull. No. 68, June 30, 1932, pp. 3, 136, 141. "Type.—*Corbula tenuis* Sowerby."

*Type* (by original designation): *Corbula tenuis* Sowerby [*Proc. Zool. Soc. London*, May 17, 1833, p. 36. "Hab. in Americâ Centrali." "One specimen was dredged among sandy mud at a depth of twelve fathoms in the Bay of Montijo."—Reeve, Conch. Icon., Vol. 2, *Corbula*, September, 1843, species 13, pl. 2, fig. 13. Original locality cited. Also described as *Corbula glypta* Li, *Bull. Geol. Soc. China*, Vol. 9, No. 3, October, 1930, p. 264, pl. 5 figs. 38, 38a. Dredged in 10-40 feet in mud at the mouth of the Rio Grande near La Boca about one mile from the mainland in Panama Bay].

Shell usually thin, inequilateral, subequivalve; posterior side contracted, with a strong, cord-like posterior keel, defining the posterior area which is more coarsely sculptured than the rest of the valve surface; a smaller secondary keel in the middle, defines an escutcheon-like area; no lunule; posterior side obliquely truncate and bicarinate at the end; hinge normal with a strong cardinal tooth in right valve, the ligament pit notch-like, small and seemingly passing internally beneath the beaks; in the left valve, a grooved posterior cardinal; external sculpture of fine, concentric threads coarser on the posterior area. (Original description).

### ***Aloidis* (*Tenuicorbula*) *fragilis*** Hinds.

*Corbula fragilis* Hinds, *Proc. Zool. Soc. London*, November, 1843, p. 56. "Hab. West coast of Veragua; from eighteen fathoms, mud." "Cab. Belcher."—Reeve, Conch. Icon., Vol. 2, *Corbula*, January, 1844, species 19, pl. 3, fig. 19. Type locality cited.—Hinds, Zool. Voy. Sulphur, Moll., Pt. 3, 1844 [January, 1845, on cover of Pt. 3], p. 68, pl. 20, fig. 11. Original locality cited.

*Type Locality*: West coast of Veragua, Panama. in 18 fathoms, mud.

*Range*: Gulf of California, to Panama.

*Collecting Station*: Mexico: Santa Inez Bay, Gulf of California (145-D-1-3), 4-13 fathoms, sand.

*Description*: Shell ovate, thin, white, striated, transverse striae very finely reticulated, anteriorly subproduced, rounded, posteriorly elongated, subrotund at umbos; ventral margin of right valve acute, produced; umbos straight, smooth, equal. Long. 7; lat. 3; alt. 4 lin. (Free translation of original description).

The thin, delicate, subequivalve, ovately diamond-shaped shell and the sculpture consisting of fine reticulate striae are characteristic features of this species.

*Distribution*: A couple of somewhat worn

specimens dredged by the expedition in Santa Inez Bay in the Gulf of California have been referred questionably to *Aloidis fragilis.* Dall, 1921, reported the species as ranging from Monterey Bay, California, to Panama, but we have not seen specimens from other than tropical or subtropical west American waters. It has been recorded as occurring in the Pleistocene of Magdalena Bay, Lower California, and near Tomales Bay, California, but specimens assigned to this species from those localities in the collections studied by us appear to be referable to *Aloidis porcella* Dall or related species.

### Family Hiatellidae.

Revisions or lists of the species of the family Hiatellidae [Saxicavidae] have been published by Tryon[82] and by Lamy.[83]

### Genus **Hiatella** Daudin.

*Hiatella* Daudin in Bosc, Hist. Nat. des Coquilles, Vol. 3, AN X [1801], p. 120. Species cited: *Hiatella biaperta,* p. 120, pl. 21, fig. 2. "Se trouve sur la côte de Tranquebar" and *Hiatella monoperta,* p. 121, pl. 21, fig. 1. "Se trouve sur les côtes de Tranquebar."—Iredale, *Rec. Australian Mus.*, Vol. 17, No. 9, June 27, 1930, p. 406.—Powell, Shellfish of New Zealand, 1937, p. 61. Type, *Mya arctica* Linnaeus.—Cotton & Godfrey, Handbook of Flora and Fauna of South Australia issued by South Australian branch of Brit. Sci. Guild (Adelaide), 1938, p. 284. "Genotype—*H. arctica* Linné".

*Saxicava* Fleuriau-Bellevue, *Journ. de Physique de Chimie, d'Hist. Nat. et des Arts,* Tome 54 (AN X), May, 1802, p. 354. "La saxicave striée, *saxicava striata*". On p. 349, "Quatrieme Genre." "Saxicave" and "*Saxicave striée.*" "Perce les rochers des côtes de la Rochelle."—Fleurieu-Bellevue, *Bull. des Sci. par la Soc. Philomathique* (Paris), Tome 3, No. 62, 1802, p. 107. "IV^e^. Genre. Saxicave, Saxicava." "Espèce. Saxicave striée."—Children, *Quart. Jour. Sci. Lit. and Arts,* Vol. 14, 1823, p. 302. Reprint by Kennard, Salisbury & Woodward, *Smithson. Miscell. Coll.*, Vol. 82, No. 17 (Publ. 3112), 1931, p. 7. Type indicated as "*S. rugosa* (*Mytilus rugosus.* Linn.)."—Dall, *Trans. Wagner Free Inst. Sci.*, Vol. 3, Pt. 4, April, 1898, p. 833. Type, *Mya arctica* Linnaeus.—Lamy, *Journ. de Conchyl.*, Vol. 68, No. 3, 1924, p. 218. Type: *Saxicava striata* Fl.=*Mya arctica* Linnaeus. —Grant & Gale, *Mem. San Diego Soc. Nat. Hist.*, Vol. 1, 1931, p. 427. Type (as designated by Children): *Mytilus rugosus* Linnaeus, 1867.

*Didonta* Schumacher, Essai Nouv. Syst. Test., 1817, pp. 42, 125, pl. 6, fig. 2 (a, b). Species cited: *Didonta bicarinata* Schumacher, Reference to *Solen minutus* Linnaeus, Chemnitz, Neues Syst. Conchyl.-Cab., Bd. 6, 1782, p. 67, Tab. 6, figs. 51, 52. [=*Mya arctica* Linnaeus].

*Type* (here designated): *Hiatella biaperta* Bosc. [Hist. Nat. des Coq., Vol. 3, AN X [1801], p. 120, pl. 21, fig. 2. "Se trouve sur la côte de Tranquebar." [=*Mya arctica* Linnaeus.].

Shell small, irregular, very inequilateral, the young with a cardinal tooth like *Panomya,* the adult with the teeth obsolete; pallial line discontinuous, siphons naked, slightly separated at the tips and in normal specimens completely retractile, shell burrowing, or nestling in gravel or broken shell, or perforating rocks, corallines, or dead shells like pholads. (Description of *Saxicava* by Dall).

We have used the name *Hiatella* Daudin instead of *Saxicava* Fleuriau de Bellevue because the date of publication of *Hiatella* given by Sherborn and by Iredale indicates that it is the earlier name. Unless a ruling in favor of suspension of the rules of nomenclature is obtained in the present case there appears to be no grounds for rejecting the name *Hiatella.* We have selected *Hiatella biaperta* Bosc, one of the two original species, as the type. Gray, 1847, selected *Solen minutus* as the type but that species was not included in the two species originally cited under *Hiatella.* Lamy and others have placed *Hiatella biaperta* in the synonymy of *H. arctica. Saxicava* thus becomes a virtual synonym of *Hiatella.**

Unless well preserved, the species of *Hiatella* are sometimes difficult to separate due to the shapes assumed by these burrowing or nestling forms.

### **Hiatella arctica** Linnaeus.

*Mya arctica* Linnaeus, Syst. Nat., ed. 12, 1767, p. 1113. "Habitat in Oceano Norvegico."—Hanley, Ipsa Linn. Conch., 1855, p. 28. Also p. 461.

*Solen minutus* Linnaeus, Syst. Nat., ed. 12, 1767, p. 1115. "Habitat in O. Norvegico. Martin."—Chemnitz, Neues Syst. Conchyl.-Cab., Bd. 6, 1782, p. 67, pl. 6, figs. 51, 52. Iceland; Greenland; Norway. Shallow and deep water.—Hanley, Ipsa Linn. Conch., 1855, p. 32. Also p. 462.

*Hiatella biaperta* Bosc, Hist. Nat. Coq., Vol. 3, AN X [1801], p. 120, pl. 21, fig. 2. "Se trouve sur la côte de Tranquebar."

*Hiatella monoptera* Bosc, Hist. Nat. Coq., Vol. 3, AN X [1801], p. 120, pl. 21, fig. 1. "Se trouve sur les côtes de Tranquebar."

*Didonta bicarinata* Schumacher, Essai Nouv. Syst. Test., 1817, p. 125, pl. 6, figs. 2a, 2b.

*Hiatella arctica* Linnaeus, Lamarck, Anim. s. Vert., Vol. 6, 1819, p. 30. "Habite les mers du Nord, dans le sable, et se rencontre parmi les fucus."

*Saxicava arctica* Linnaeus, Philippi,

[82] Tryon, Jr., G. W. Catalogue of the Families Saxicavidae, Myidae and Corbulidae. *Amer. Jour. Conch.*, Vol. 4, Pt. 5, ap., May 6, 1869, pp. 59-68. Saxicavidae, pp. 59-60.

[83] Lamy, E. Révision des Saxicavidae vivants du Muséum national d'Histoire Naturelle de Paris. *Journ. de Conchyl.*, Vol. 68, No. 3, October, 1924, pp. 218-248; Vol. 68, No. 4, March, 1925, pp. 261-283.

* A paper by Henry Dodge entitled "Hiatella Daudin Versus Saxicava Bellevue" (*Nautilus*, Vol. 64, No. 1, July, 1950, pp. 29-33), appeared after the present paper was submitted for publication.

Enum. Moll. Sicil., Vol. 1, 1836, p. 20, pl. 3, figs. 3, 3a-d. Sicily. Recent and fossil.—Forbes & Hanley, Hist. Brit. Moll., Vol. 1, 1853 (issued April 1, 1848), p. 141, pl. 6, figs. 4-6. Great Britain. Boreal and Arctic regions of the north Atlantic. Rarely in Mediterranean.—Sowerby, Conch. Icon., Vol. 20, *Saxicava*, 1875, species 1, pl. 1, figs. 1a, 1b, 1c, 1d. Arctic regions, British and North American coasts.—Sars, Bid Kunds. Norges Arkt. Fauna. I. Moll. Reg. Arct. Norvegiae, 1878, p. 95, pl. 20, figs. 8a, 8b, 8c. Norway and Arctic regions.—Clessin, Conchyl.-Cab. Martini-Chemnitz, Bd. 11, Abt. 4a, Saxicavidae, 1895, p. 37, pl. 7, figs. 1-3.—Bucquoy, Dautzenberg & Dollfus, Moll. Mar. Roussillon, Vol. 2, Fasc. 11, 1896, p. 589, pl. 86, figs. 1-4; 5-11 (var.). Mediterranean; Atlantic from Norway to the Cape of Good Hope and St. Helena. Japan, Western America, Australia, New Zealand (Smith) [with synonymy].—I. S. Oldroyd, *Stanford Univ. Publ. Univ. Ser. Geol. Sci.*, Vol. 1, 1924, p. 208, pl. 9, fig. 6; pl. 51, fig. 4. Arctic Ocean to Panama. Also Atlantic—Lamy, *Journ. de Conchyl.*, Vol. 68, No. 3, 1924, p. 222. Numerous localities cited.—Grant & Gale, *Mem. San Diego Soc. Nat. Hist.*, Vol. 1, 1931, p. 427. Earlier records cited. Miocene to Recent.

*Type Locality*: Norwegian seas.

*Range*: Arctic Ocean to Panama. Also Mediterranean; Atlantic from Norway to the Cape of Good Hope; western Atlantic from the Arctic to the West Indies.

*Collecting Stations*: Mexico: Port Guatulco (195-D-9), 7 fathoms, gr. sand, crushed shell; Nicaragua: Corinto (200-D-19), 12-13 fathoms, mangrove leaves; Costa Rica: Piedra Blanca Bay (208-D-1, 10), 2-6 fathoms, rocks, sand, algae.

*Description*: "M. testa striata: valvulis carinis duabus spinulosis; cardine edentulo. Habitat in Oceano Norvegico. *F. Zoega.* Testa magnitudine Fabae, rudis, facie Arcae noae, pallida. Antice retuso-planiuscula, parte anteriore obtusissima, posteriore breviore, acutiuscula; pars interior a natibus excurrit angulis duobus remotis antrorsum subaculeatis. Cavitas interna lactea est. Cardo vix ullus." (Linnaeus. Original description).

A left valve in the present collection from Costa Rica measures approximately 20 mm. in length and 10 mm. in height.

The shell of *Hiatella arctica* differs from that of *H. pholadiformis* Linnaeus in the more compressed, squarely rectangular shape with the posterior end as wide as the anterior, in the presence of one or two radiating ridges ornamented with scaly spines, in that the beaks are nearer the anterior end, and in the presence of a tooth in the left valve. The posterior end of *H. pholadis* is usually tapering and the hinge is usually without teeth. Sars has given good illustrations showing the hinges of these two species. The foregoing criteria may not always serve to separate the two species but with shells not extremely irregular and especially on those showing the young stages of growth some of the features mentioned usually serve to separate the two forms.

*Hiatella arctica* is very similar to *H. rugosa* Linnaeus, a species occurring in the North Atlantic and Mediterranean. According to Bucquoy, Dautzenberg & Dollfus *H. rugosa* lives in shallower water and has no byssus. Other features said to be characteristic of *Hiatella rugosa* are lack of radiating carinations except on the summits of the umbos and the absence of hinge teeth.

*Hiatella antarctica* Philippi[84], regarded by some authors as a subspecies of *H. arctica*, is a similar form occurring in the Magellanic and Antarctic regions.

*Hiatella hawaiensis* Dall, Bartsch & Rehder[85], recently described from Hawaii, is said to differ from *H. arctica* in possessing a more rugose shell in which the teeth are virtually lacking.

In addition to *Hiatella arctica*, at least six other species of "*Saxicava*" have been cited as occurring in tropical west American waters. These are *Saxicava pholadis* Linnaeus, *S. purpurascens* Sowerby, *S. solida* Sowerby *S. tenuis* Sowerby, *S. acuta* De Folin and *S. initialis* De Folin.

*Distribution*: A few specimens apparently referable to *Hiatella arctica* were collected by the expedition off Mexico, Nicaragua and Costa Rica. It has been recorded from many localities in the Pacific from the Arctic Ocean to Panama and from Miocene to Recent. It also has a wide distribution in the Arctic and Atlantic Ocean.

## FAMILY GASTROCHAENIDAE.

A synopsis of the Recent species of this family has been published by Tryon[86] and a revision of a number of the living species has been published by Lamy[87]. Philippi[88] and Kühnelt[89] have made special studies of the anatomy and biology of some of the species in this family.

Dall, 1898, stated that "*Gastrochaena*" extends well into the Mesozoic. The genus has been cited from the upper Cretaceous of

[84] *Saxicava antarctica* Philippi, *Archiv f. Naturgesch.*, Jahrg. 11, Bd. 1, 1845, p. 51. "Patria: Insulae Chonos infra Chiloe."—Hedley, Australasian Antarct. Exped. 1911-1914. *Sci. Repts. Ser. C*, Vol. 4, Pt. 1, November 6, 1916, p. 33, pl. 4, figs. 51, 52, 53. Macquarie Island in the Antarctic.

[85] *Saxicava hawaiensis* Dall, Bartsch & Rehder, *Bernice P. Bishop Mus., Bull.* 153, July 25, 1938, p. 200, pl. 50, figs. 13 and 14. Dredged "on a coral reef, at Fort Armstrong, Oahu, 8-15 feet."

[86] Tryon, Jr., G. W. Synopsis of the Recent Species of Gastrochaenidae, a Family of Acephalous Mollusca. *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 13, March 31, 1862, pp. 465-494.

[87] Lamy, E. Révision des Gastrochaenidae vivants du Muséum National d'Histoire Naturelle de Paris. *Journ. de Conchyl.*, Vol. 68, No. 4, March 20, 1925, pp. 284-319.—Notes sur les espèces Lamarckiennes appartenant à la famille des Gastrochaenidae. *Bull. Mus. Nat. d'Hist. Nat. (Paris)*, Vol. 28, 1922, pp. 307-311.

[88] Philippi, R. A., *Archiv f. Naturgesch.*, Jahrg. 11, Bd. 1, 1845, pp. 185-188, pl. 7, figs. 1-10.

[89] Kühnelt, W., *Palaeobiol.*, Bd. 5, Lief. 3, 1933, pp. 386-395.

Libya by Quaas[90] and from California by Packard[91].

*Kummelia* Stephenson[92], with the type *Gastrochaena americana* Gabb, has been described from the Rancocas group, Eocene of New Jersey.

### Genus **Rocellaria** Blainville.

*Rocellaria* Blainville, Dict. Sci. Nat. (Levrault), Vol. 57, 1828 (issued January 10, 1829), p. 244. Sole species: *G. modiolina* Lamarck.—Tryon, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 13, March 31, 1862, p. 477. —Iredale, *Proc. Malacol. Soc. London*, Vol. 11, Pt. 5, 1915, p. 297. "Type (by monotypy): *G. modiolina*, Lamk.=*Mya dubia*, Pennant." —Prashad, Siboga Exped., Monogr. 53c, 1932, Lamell., p. 315. Type, *Rocellaria dubia* Pennant.—Dall, Bartsch & Rehder, *Bernice P. Bishop Mus., Bull.* 153, July 25, 1938, p. 201. "Type: *Gastrachaena modiolina* Lamarck=*Mya dubia* Pennant (by monotypy)."

*Type* (by monotypy): *Gastrochaena modiolina* Lamarck [Hist. Nat. Anim. s. vert., Vol. 5, July, 1818, p. 447. "Habite près de la Rochelle et sur les côtes d'Angleterre." Reference to *Mya dubia* Pennant, Zool. Brit., Vol. 4, pl. 44, fig. 19, and Encycl. Meth., pl. 219, figs. 3 and 4 "Non bene."—Forbes & Hanley, Hist. Brit. Moll., Vol. 1, 1853 (issued April 1, 1848), p. 132, pl. 2, figs. 5, 6, 7, 8; and (animal) pl. F, fig. 5. Great Britain. (=*Mya dubia* Pennant, Brit. Zool., Vol. 4, 1777, p. 82, pl. 44, fig. 19. Also illustrated by Sowerby, Conch. Icon., Vol. 20, *Gastrochaena*, 1878, pl. 1, figs. 1a-c, and by Sowerby, Thes. Conch., Vol. 5, 1884, p. 127, pl. 470, fig. 2. British and Mediterranean coasts)].

Shell of small to medium size, ovate with the anterior end pointed and with the ventral margin below the point strongly gaping; the shell is moderately thin, inflated and white in color, with the umbones near the anterior end. The surface is covered with strong concentric incremental lines or wrinkles, which are often lamellar. Ligament external, posterior, moderately long. Hinge line rather straight, somewhat thickened, toothless. The interior is white, with a large ovate posterior and a small, ovate anterior muscle scar; the pallial sinus is moderately deep and rather sharply angular. (Dall, Bartsch & Rehder).

Dall, 1898, pointed out that species of this genus form "flask-shaped excavations (chiefly in shells and corals) which are lined with calcareous matter, or when not protected by a burrow, forming a partial or complete shelly tube to which extraneous matter is attached."

The west American shells here included under the genus *Rocellaria* Blainville were by earlier authors referred to *Gastrochaena* Spengler. Iredale (1915) has given reasons for accepting *Rocellaria* with the type *Gastrochaena modiolina* Lamarck (=*Mya dubia* Pennant) for shells of this group. The genus *Gastrochaena* Spengler[93] with the type *Gastrochaena mumia* Spengler includes shells whose characters differ somewhat from those of *Rocellaria*. This usage of *Gastrochaena* includes *Fistulana* of recent authors.

In western North America "*Gastrochaena*" *dubitata* M. A. Hanna, 1927, has been described from the Eocene and species referable to *Rocellaria* have been recorded in the Pleistocene and Recent.

In eastern North America *Rocellaria* occurs at least as early as the Miocene and perhaps in the Eocene.

Dall, Bartsch & Rehder, 1938, have recently described three new species of this genus from the Hawaiian Islands, *R. hawaiensis*, *R. kanaka* and *R. oahuana*.

### **Rocellaria ovata** Sowerby.

Plate II, Fig. 2.

*Gastrochaena ovata* Sowerby, *Proc. Zool. Soc. London*, June 17, 1834, p. 21. "Hab. in Sinu Panamensi (Isle of Perico,) et ad Insulam Platae." "Found in *Spondyli* at the Isle of Perico, and in coral rocks, at a depth of seventeen fathoms, at the island of Plata." —Tryon, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 13, March 31, 1862, p. 481.—Sowerby, Conch. Icon., Vol. 20, 1878, *Gastrochaena*, species 16, pl. 3, figs. 16a, 16b. "Hab. Panama."—Sowerby, Thes. Conch., Vol. 5, 1884, *Gastrochaena*, p. 128, pl. 470, fig. 9. Panama. —Lamy, *Journ. de Conchyl.*, Vol. 68, No. 4, 1925, p. 304. The Carolinas to the West Indies on the Atlantic coast, and from the Gulf of California to Ecuador on the Pacific coast.

*Type Locality*: Island of Perico, Bay of Panama, in *Spondyli* (here designated as type locality). Also cited originally from the Island of La Plata, Ecuador, in 17 fathoms, in coral rock.

*Range*: Scammon Lagoon, Lower California, to the Gulf of California and south to the Island of La Plata, Ecuador. Also in the Atlantic from South Carolina to the West Indies.

*Collecting Stations*: Mexico: Arena Point, Lower California; Port Guatulco (195-D-15), 1.5 fathoms, coral; Costa Rica: Uvita Bay, in coral heads.

*Description*: Gast. testâ ovatâ, albicante, longitudinaliter striatâ, striis exilibus, lamellosis, formam marginis semper sequentibus; longitudine lateris antici quintam

[90] *Gastrochaena* sp., Quaas, *Palaeontogr.*, Bd. 30, Th. 2, Lief. 4, November, 1902, p. 232, Tab. 25, figs. 16a, b, 17a, b. Lower Danian (overwegischichten) in Libyschen Wüste.

[91] *Gastrochaena* sp., Packard, *Univ. Calif. Publ. Bull. Dept. Geol. Sci.*, Vol. 13, No. 10, June 30, 1922, p. 428, pl. 31, fig. 1.

[92] *Kummelia* Stephenson, *Jour. Washington Acad. Sci.*, Vol. 27, No. 2, February 15, 1937, p. 60. See also Stephenson's remarks on *Gastrochaena* and related genera (*Univ. Texas Publ.* No. 4101, October, 1941, pp. 242-244.

[93] *Gastrochaena* Spengler, *Nye Saml. K. Danske Vidensk.-Selsk. Skrifter* (Kjoben.), Vol. 2, 1783, p. 179. Species cited include *Gastrochaena mumia*, *G. cuneiformis*, and *G. cymbium*. Iredale, 1915, considered H. & A. Adams (Gen. Rec. Moll., Vol. 2, June, 1856, p. 335) as fixing the type of *Gastrochaena* when they cited *G. mumia* Spengler as an example and stated "The curious shell on which Spengler founded this genus is generally known under the name of *Fistulana clava*, Lamarck; it is also the type of the *Chaena* of Retzius." Stoliczka (*Mem. Geol. Surv. India. Palaeont. Indica*, (Ser. 6, Vol. 3). Cret. Fauna South. India, Vol. 3, 1870, p. XV), definitely designated *Gastrochaena mumia* Spengler as type.

partem testae aequante: long. 1.2, lat. 0.7, alt. 0.7 poll. (Original description).

Ovate, whitish, with concentric striae, which are slender, lamellar, and following the shape of the margin: anterior side quadruple the length of the posterior, and rounded at the extremity: gape very large. 7/10 . . . 1⅕ [inches]. (Hanley, Cat. Rec. Biv. Shells, 1843, pp. 10-11).

Tryon summarized the criteria useful in separating *Rocellaria ovata* from other similar forms as follows: "The great difference in the relative length of the anterior and posterior sides will readily distinguish this species from *R. brevis*. *R. dubia* has a slight truncation of the posterior margin of the valves, while this species is always rounded posteriorly. The absence of the laminar hinge-plate and the length of the hiatus also separate this shell from both *R. dubia* and *R. hians*."

*Rocellaria rotunda* Dall[94] was originally described as a variety of *R. ovata* from the Bowden formation, Jamaica, Miocene. It has also been recorded as occurring in the Miocene of Florida and Costa Rica. Compared to the Recent species *R. ovata*, the fossil form is said to be smaller, thinner, with a more elongate form and a more distinct myophore.

*Distribution*: A few specimens of this species were taken by the expedition in the Gulf of California, at Port Guatulco, Mexico, and at Uvita Bay, Costa Rica. This is one of the species which occurs both in Pacific and Atlantic waters. Tryon stated, "I have made a very close comparison between specimens from Panama and those from the West Indies and Charleston, without detecting the slightest difference between them."

## SUPERFAMILY ADESMACEA.

Key to the genera and subgenera of the Adesmacea.

- A. Anterior margin incised to form approximately a right angle
  - a. Pallets present at siphonal end
    - b. Pallets simple, fork-shaped, or paddle-shaped .................... *Teredo*[95]
    - bb. Pallets compound, feather-like in appearance ........................ *Bankia*[95]
  - aa. Pallets absent .................... *Xylophaga*[95]
- B. Anterior margin not forming a definite angle
  - a. With a furrow dividing the shell into roughened anterior and smooth posterior areas
    - b. Anterior gape in adult shell closed by a callum
      - c. Dorsal margin doubled or reflected both anterior and posterior to beaks ........... *Parapholas*
      - cc. Dorsal margin doubled or reflected only anterior to beaks or not at all
        - d. With elongate median ventral accessory plate
          - e. Very short, subglobose; inequivalve, callum of left valve overlapping that of right *Jouannetia*
            - f. Two impressed radiating grooves (subgenus) *Jouannetia s.s.*[95]
            - ff. One impressed radiating groove (subgenus) *Triomphalia*
          - ee. Elongate, equivalve *Martesia*
        - dd. Without ventral accessory plate
          - g. Accessory plate above umbos present .... (subgenus) *Penitella*[95]
          - gg. Accessory plate above umbos lacking ..*Pholadidea*[95]
    - bb. Anterior gape in adult shell not closed by a callum
      - h. Accessory plates rudimentary or lacking
        - i. Shell large, coarse *Zirfaea*[95]
        - ii. Shell small; subglobose; posterior end very short; anterior margin thickened and dentate *Navea*[95]
      - hh. Accessory plates well developed
        - j. 2 small accessory plates in front of beaks only; shell very thin; posterior end much produced (subgenus) *Nettastomella*[95]
        - jj. 1 large acces-

[94] For references to this species see Gardner, J., *U. S. Geol. Surv., Prof. Paper* 142-E, 1928, p. 238.

[95] Not represented in the present collection.

sory plate in front of beaks and 1 narrow plate back of beaks *Hiata*[95]

aa. Without a furrow; callum lacking

k. Reflected margin of shell divided into two layers which are separated by about 12 vertical partitions ..................... *Pholas*[95]

kk. Reflected margin of shell undivided ........................... *Barnea*

### Family Pholadidae.

Important papers dealing with this family have been published by Tryon[96] and Lamy.[97]

### Genus **Barnea** Leach.

#### **Barnea pacifica** Stearns.

*Pholas pacifica* Stearns, Conch. Memoranda, No. 7, August 28, 1871, p. 1. Republished in *Proc. Calif. Acad. Sci.*, Vol. 5, May, 1873, p. 81, pl. 1, figs. 6, 6a, 6b, 6c. "Habitat.—Alameda, San Francisco Bay, California, where in some places it is common in sandy mud between tide marks."

*Barnea pacifica* Stearns, I. S. Oldroyd, *Stanford Univ. Publ. Univ. Ser. Geol. Sci.*, Vol. 1, 1924, p. 209, pl. 21, figs. 2, 3, 4. (Copy of Stearns' illustrations). San Francisco Bay to Lower California.

*Type Locality*: Alameda, San Francisco Bay, California, in sandy mud between tide marks.

*Range*: San Francisco Bay, California, to Peru.

*Collecting Station*: Nicaragua: Corinto (200-D-19), 12-13 fathoms, mangrove leaves.

*Description*: A small right valve 19.5 mm. in length appears referable to this species. The dorsal and ventral margins are subparallel. It is ornamented with fine radial and concentric sculpture which, where the two cross, form fine scaly projections on the anterior ventral area. The anterior end is subangulate, the anterior vental margin obliquely truncated; the posterior end is truncated, slightly rounded above, broadly so below.

The anterior end of the present specimen is less pointed than that of young specimens of *Barnea pacifica* in the Henry Hemphill collection in the California Academy of Sciences. This feature, perhaps, may vary in a series of specimens.

Lamy placed *Barnea pacifica* in the synonymy of *B. spathulata* Deshayes,[98] a species originally described from Chile. We have not seen specimens from Chile but judging from the illustration, it appears that the posterior end of *B. spathulata* is a little more rounded than that of *B. pacifica*. We are uncertain whether or not Stearns' species, described from San Francisco Bay, California, is identical with *B. spathulata* and we have therefore referred the present specimens to *B. pacifica*. Olsson[99] cited *B. pacifica* from Peru and Gigoux[100] cited it from Chile.

According to the original description of *Barnea subtruncata* Sowerby,[101] that species is very close to *S. parva* Pennant, a north European species. The anterior end of *B. parva* is much more attenuated and the posterior end is more tapering and rounded than that of the present specimen. The type of *B. subtruncata* has not been illustrated but the illustration of *B. lamellosa* d'Orbigny,[102] a form placed by Dall[103] in the synonymy of *B. subtruncata* and considered by Lamy to be a subspecies of *B. subtruncata*, does bear a strong resemblance to *B. parva*.

*Distribution*: A single small valve of this species was dredged by the expedition at Corinto, Nicaragua, in 12-13 fathoms.

### Genus **Jouannetia** des Moulins.

A systematic review of a number of species of the genus *Jouannetia*, especially fossil forms, has been published by Sieverts.[104]

### Subgenus **Triomphalia** Sowerby.

#### **Jouannetia (Triomphalia) pectinata** Conrad.

Plate II, Fig. 6.

*Pholadopsis pectinata* Conrad, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 4, 1849, p. 156. [No locality cited but the shells described were "from the coasts of Lower California and Peru."].—Conrad, *Jour. Acad. Nat. Sci. Philadelphia*, Ser. 2, Vol. 1, January, 1850, p. 279, pl. 39, fig. 3. Original localities cited.

---

95 Not represented in the present collection.

96 Tryon, Jr., G. W. On the Classification and Synonymy of the Recent species of Pholadidae. *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 14, 1862, pp. 191-221. See also Dall, W. H., *Trans. Wagner Free Inst. Sci.*, Vol. 3, Pt. 4, April, 1898, pp. 814-823.

97 Lamy, E. Révision des Pholadidae vivants du Muséum National d'Histoire Naturelle de Paris. *Journ. de Conchyl.*, Vol. 69, No. 1, July 5, 1925, pp. 19-51; Vol. 69, No. 2, October 10, 1925, pp. 79-103; Vol. 69, No. 3, January 31, 1926, pp. 136-168, 3 figs. in text; Vol. 69, No. 4, May 15, 1926, pp. 193-222.

98 *Pholas spathulata* Deshayes, *Mag. de Zool.*, Guerin-Menev., Vol. 5, Moll., 1843, pl. 79, p. 1 [two figs.]. "Habite les mers du Chili."

Not *Pholas spathulata* Sowerby, *Proc. Zool. Soc. London* for 1849, p. 162 (issued between January and June, 1850). "From New Zealand." Renamed *Pholadidea suteri* by Lamy, 1925.

*Barnea (Cyrtopleura) spathulata* Deshayes, Lamy, *Journ. de Conchyl.*, Vol. 69, No. 2, 1925, p. 89. Payta, Peru; Chile.

99 Olsson, A. A., *Nautilus*, Vol. 37, No. 4, 1924, p. 130. Paita and Lobitos, Peru.

100 Gigoux, E. E., *Rev. Chilensis Hist. Nat.*, Vol. 38, 1934, p. 285. Atacama, Chile.

101 *Pholas subtruncata* Sowerby, *Proc. Zool. Soc. London*, November 25, 1834, p. 69. "Hab. ad Insulam Platae, Columbiae Occidentalis." "Found in soft stone at a depth of seventeen fathoms. Very like our British *Pholas parva*." See also *Barnea (Anchomas) subtruncata* Sowerby, Lamy, *Journ. de Conchyl.*, Vol. 69, No. 2, 1925, p. 82.

102 *Pholas lamellosa* d'Orbigny, Voy. Amér. Mérid., Vol. 5, Moll., 1846, p. 498, pl. 77, figs. 20, 21 . . . "sur toute la côte de Patagonie, au sud du Rio Negro, au niveau des marées ordinaires de vives eau. Elle se creuse un trou dans les couches de grès friable et de calcaires."

103 Dall, W. H., *Proc. U. S. Nat. Mus.*, Vol. 37, 1909, p. 276.

104 Sieverts, H. Beiträge zur Paläontologie des Ostindischen Achipels. IX. *Jouannetia cumingi* (Sowerby) aus dem Pliocän von Timor. Nebst Bemerkungen über andere Arten dieser Gattung. Neues Jahrb. f. Min. Geol. und Paläo., Beil. Bd. 71, Abt. B, Heft 2, 1933, pp. 267-302, 2 text-figs.

*Triomphalia pulcherrima* Sowerby, *Proc. Zool. Soc. London* for 1849, p. 161, pl. 5, figs. 2, 2a, b, c, d, (issued between January and June, 1850). "Found in soft stone at low water at West Colombia; Cuming."—Sowerby, Thes. Conch., Vol 2, 1849, p. 501, pl. 106, figs. 58, 59. Original locality cited.

*Jouannetia pulcherrima* Sowerby, Chenu, Man. de Conchyl., Vol. 2, 1862, p. 8, fig. 37.

*Pholas pulcherrima* Sowerby, Sowerby, Conch. Icon., Vol. 18, *Pholas*, August, 1872, species 44, pl. 11, fig. 44. Original locality cited.

*Jouannetia (Triomphalia) pectinata* Conrad, Lamy, *Journ. de Conchyl.*, Vol. 69, No. 4, 1926, p. 219. Acapulco, Mexico.

*Type Locality*: East coast of Lower California (here designated as type locality). Exact locality not cited originally but the shells described were "from the coasts of Lower California and Peru." Of *Triomphalia pulcherrima*, West Colombia.

*Range*: Acapulco, Mexico, to Peru.

*Collecting Station*: Costa Rica: Port Parker.

*Description*: Ovate, very thin and fragile, profoundly gaping posteriorly; profoundly ventricose anteriorly; valves with elevated waved laminae terminating near a profound sinus, which extends from beak to base; right valve undulated near the posterior end, reflected, margin pectinated; both valves have concentric lines. (Original description).

A right valve in the present collection measures approximately: length, 29 mm.; height (incomplete), 21 mm.; convexity (one valve, incomplete), 10 mm.

The concentric sculpture on the posterior portion of a left valve in the present collection is crossed by faint radiating lines. Radial sculpture is not present on the corresponding area of the right valve. However, the present specimens are not perfectly preserved. The posterior margins of the valves show traces of the pectinated sculpture mentioned by Conrad as present on the shell of this species.

*Distribution*: Two single valves of this species were collected by the expedition at Port Parker, Costa Rica.

### Genus **Parapholas** Conrad.

#### **Parapholas calva** Gray in Sowerby.

*Pholas calva* Gray MS., Sowerby, *Proc. Zool. Soc. London*, November 25, 1834, p. 69. "Hab. ad Sinum Panamae." "Found in *Spondyli*, at a depth of twelve fathoms, at the Isle of Perico in the Bay of Panama: the young shells have also been taken out of hard stones at low water in the same place."—Sowerby, Thes. Conch., Vol. 2, 1849, p. 493, pl. 105, figs. 51-53. "Collected by Mr. Cuming in very hard stone at low water, in Panamá Bay."—Sowerby, Conch. Icon., Vol. 18, *Pholas*, March, 1872, species 20, pl. 5, fig. 20. [Same locality record as in preceding reference].

*Parapholas bisulcata* Conrad, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 4, 1849, p. 156. [No exact locality cited but shells were described "from the coasts of Lower California and Peru"].—Conrad, *Jour. Acad. Nat. Sci. Philadelphia*, Ser. 2, Vol. 1, 1850, p. 279, pl. 39, fig. 5. [Not fig. 4]. Original localities cited.

*Martesia calva* Sowerby, Chenu, Man. de Conchyl., Vol. 2, 1862, p. 9, figs. 45, 46, 47.

*Parapholas calva* Sowerby, Lamy, *Compt. Rend. Congress Soc. Savantes*, Paris, 1924, p. 248. Panama.—Lamy, *Journ. de Conchyl.*, Vol. 69, No. 3, 1926, p. 165.

*Type Locality*: Island of Perico in the Bay of Panama, in 12 fathoms, in *Spondylus*.

*Range*: Corinto, Nicaragua, to Panama. Probably to Peru.

*Collecting Station*: Nicaragua: Corinto (200-D-19), 12-13 fathoms, mangrove leaves.

*Description*: A right valve in the present collection, approximately 25 mm. long, appears to be referable to *Parapholas calva*. The imperfect preservation and lack of dorsal plates leaves positive identification of the specimen open to doubt but the shape and ornamentation agree more nearly with this than with any other species. The narrow tapering posterior end is rounded and not sharply acuminate like that of *P. acuminata* Sowerby.[105] A variety, *Parapholas calva* var. *nana*[106] Sowerby, also was described from Panama.

*Distribution*: A single small and somewhat worn valve here referred to *Parapholas calva* was dredged by the expedition at Corinto, Nicaragua, in 12-13 fathoms.

### Genus **Martesia** Leach.

Key to the species of *Martesia*.

A. Sculpture on anterior area fine; dorsal plate projects deeply between valves *intercalata*

B. Sculpture on anterior area moderately coarse; dorsal plate not projecting deeply between valves ................................... *curta*

#### **Martesia curta** Sowerby.

*Pholas curta* Sowerby, *Proc. Zool. Soc. London*, November 25, 1834, p. 71. "Hab ad littora Columbiae Occidentalis." "From the Isle of Lions, Province of Veragua, in soft stone at low water."—Sowerby, Thes. Conch., Vol. 2, 1849, p. 494, pl. 104, figs. 33, 34; pl. 108, fig. 105. Fig. 105 from a specimen in the British Museum. The others from "... in soft stone at low water on the coast of West Colombia, by Mr. Cuming."—Sowerby, Conch. Icon., Vol. 18, *Pholas*, March, 1872, species 16, pl. 5, figs. 16a, 16b. [Same locality as in preceding reference].

*Martesia curta* Sowerby, Dall, *Proc. U. S.*

---

[105] *Pholas acuminata* Sowerby, *Proc. Zool. Soc. London*, November 25, 1834, p. 70. "Hab. ad Panamam." "Found in limestone at low water."—Sowerby, Thes. Conch., Vol. 2, 1849, p. 492, pl. 105, figs. 48, 49, 50. Original locality cited. —Sowerby, Conch. Icon., Vol. 18, *Pholas*, March, 1872, species 19, pl. 5, fig. 19. Original locality cited.

*Parapholas acuminata* Sowerby, Lamy, *Journ. de Conchyl.*, Vol. 69, No. 3, 1926, p. 163. Paita, Peru. [Not the records from California].

[106] *Pholas calva* var. *nana* Sowerby, *Proc. Zool. Soc. London*, November 25, 1834, p. 70. "Hab. ad Panamam." "Found in hard stones at low water." See also Lamy, *Journ. de Conchyl.*, Vol. 69, No. 3, 1926, p. 166. Panama.

*Nat. Mus.*, Vol. 37, 1909, pp. 161, 277. Gulf of Panama, to Tumbez, Peru. Also Atlantic and Antilles.—Lamy, *Journ. de Conchyl.*, Vol. 69, No. 4, 1926, p. 208. United States.

*Type Locality*: Island of Lions, Veragua, Panama, at low water, in soft stone.

*Range*: Magdalena Bay, Lower California, to Tumbez, Peru. Also Atlantic and Antilles (Dall).

*Collecting Station*: Nicaragua: Corinto (200-D-19), 12-13 fathoms, mangrove leaves.

*Description*: Shell elongately ovate, with a callum, rounded and ventricose anteriorly, tapering posteriorly and rounded at the end; valves divided into two areas of sculpture by a grooved band, anterior portion sculptured with concentric ridges crossed by radiating striae, posterior area with well developed concentric sculpture which becomes obsolete posteriorly; an accessory plate present anterior to the beaks; periostracum thin, light olive green.

A very small right valve about 6 mm. in length agrees well in shape and sculpture with adult specimens of *Martesia curta*. A specimen of this species in the collections of the California Academy of Sciences, collected by Mr. W. D. Clark at Tabor Island, Chame Bay, Panama, measures: length, 31 mm.; height, 15.5 mm.; convexity (both valves together), 14.5 mm.

*Distribution*: Only a single small valve, here assigned to this species, was dredged by the expedition in 12-13 fathoms off Corinto, Nicaragua.

**Martesia intercalata** Carpenter.

*Martesia intercalata* Carpenter, Cat. Mazatlan Shells, August, 1855, p. 13. "Hab. —Mazatlan; in *Spondylus Lamarckii* [=*S. calcifer*, see p. 547], extremely rare; Havre Col."—Lamy, *Journ. de Conchyl.*, Vol. 69, No. 4, 1926, p. 209. Original record cited.—Schenck, *Jour. Paleo.*, Vol. 18, No. 5, 1945, p. 519, pl. 66, figs. 17, 18. Magdalena Bay, Lower California, Mexico.

*Type Locality*: Mazatlan, Mexico, in *Spondylus calcifer.*

*Range*: Mazatlan, Mexico, to Panama.

*Collecting Station*: Nicaragua: Corinto (200-D-19), 12-13 fathoms, mangrove leaves.

*Description*: A left valve 14.5 mm. in length in the present collection is assigned to *Martesia intercalata*. The sculpture on the anterior portion of the valve is very fine and the concentric sculpture on the posterior portion is weak. A small portion of what appears to have been the umbonal shield is attached to the umbo. Carpenter stated: "The species is named from the remarkable way in which the umbonal shield pushes itself in anteriorly between the projecting portions of the closed valves; and in which the cup, which pouts out from the otherwise rounded extremity, pushes itself in between the anterior and posterior plates, cleaving them and thrusting them back".

The sculpture on the anterior end of the present specimen is finer than that on *Martesia curta* Sowerby. This sculpture is similar to that shown in the illustration of *Hiata infelix* McLean & Zetek[107] but that shell is said to completely lack a callum. M. Smith[108], 1944, placed *H. infelix* in the family Teredidae.

*Distribution*: A single left valve here assigned to *Martesia intercalata* was dredged in 12-13 fathoms at Corinto, Nicaragua. Similar specimens in the Henry Hemphill Collection in the California Academy of Sciences were secured at Panama by Newcomb.

---

[107] *Hiata infelix* McLean & Zetek, *Nautilus*, Vol. 49, No. 4, April, 1936, p. 111, pl. 8, figs. 1-4. "Balboa, Canal Zone."

[108] Smith, M., Panamic Mar. Shells (Trop. Photogr. Lab., Winter Park, Florida), 1944, p. 69, fig. 885.

## EXPLANATION OF THE PLATES.

### PLATE I.

Fig. 1. *Tagelus (Tagelus) californianus* Conrad. Hypotype, left valve from Loc. 4506 (C.A.S. H. Hemphill Coll.), San Diego, California. Length, 111.6 mm.; height, 30 mm. P. 222.

Fig. 2. *Solen pfeifferi* Dunker. Hypotype, left valve, from Station 200-D-10, Corinto, Nicaragua, Lat. 12° 27′ 46″ N., Long. 87° 11′ 32″ W., dredged in 7 fathoms (12.8 meters). Length, 34.1 mm.; height, 7.1 mm. P. 226.

Fig. 3. *Solen crockeri* Hertlein & Strong, sp. nov. Holotype, left valve, from Station 199-D-3, Monypenny Point, Nicaragua, in the Gulf of Fonseca, Lat. 13° 03′ N., Long. 87° 30′ W., dredged in 6 fathoms (11 meters). Length, 38.8 mm.; height, 10.5 mm. P. 225.

Fig. 4. *Tagelus (Tagelus) violascens* Carpenter. Hypotype (Stanford Univ. Coll.), left valve, from Salina Cruz, Oaxaca, Mexico; H. N. Lowe Coll. Length, 85 mm.; height, 30 mm. P. 223.

Fig. 5. *Solen crockeri* Hertlein & Strong, sp. nov. Holotype, right valve of the specimen shown in Fig. 3.

Fig. 6. *Tagelus (Tagelus) violascens* Carpenter. Hypotype, left valve. View of the exterior of the specimen shown in Fig. 4.

Fig. 7. *Solen crockeri* Hertlein & Strong, sp. nov. Holotype, right valve. View of the interior of the specimen shown in Fig. 5.

Fig. 8. *Tagelus (Mesopleura) politus* Carpenter. Hypotype, left valve, from Loc. 28186 (C.A.S.), Kino Bay, Sonora, Mexico, in the Gulf of California; H. N. Lowe Coll. Length 33.8 mm.; height, 10.8 mm. P. 224.

Fig. 9. *Tagelus (Tagelus) affinis* C. B. Adams. Hypotype, left valve, from Loc. 24061 (C.A.S.), Bay of Panama; F. M. Anderson Coll. Length, 58 mm.; height, 20.6 mm. P. 222.

Fig. 10. *Tagelus (Mesopleura) politus* Carpenter. Hypotype, left valve, from the same locality as the specimen shown in Fig. 8. Length, 35.1 mm.; height, 12.4 mm.

Fig. 11. *Tagelus (Tagelus) affinis* C. B. Adams. Hypotype, left valve. View of the exterior of the specimen shown in Fig. 9.

Fig. 12. *Tagelus (Mesopleura) subteres* Conrad. Hypotype, left valve, from Loc. 4509 (C.A.S. H. Hemphill Coll.), San Diego, California. Length, 39.8 mm.; height, 13.4 mm. P. 225.

Fig. 13. *Tagelus (Mesopleura) subteres* Conrad. Hypotype, left valve, from the same locality as the specimen shown in Fig. 12. Length, 45.6 mm.; height, 14.2 mm. P. 225.

Fig. 14. *Tellina (Scrobiculina) viridotincta* Carpenter. Hypotype, right valve, from Loc. 23811 (C.A.S.), Gulf of California. Length, 59.6 mm.; height, 43.3 mm.

This species was discussed in *Zoologica*, New York Zool. Soc., Vol. 34, No. 9, p. 66.

Fig. 15. *Tellina (Phyllodella) insculpta* Hanley. Hypotype, right valve, from Station 197-D-2, 7 miles west of Champerico, Guatemala, Lat. 14° 13′ N., Long. 92° 02′ W., dredged in 14 fathoms (25 meters). Length, 34.6 mm.; height, 18.7 mm.

This species was discussed in *Zoologica*, New York Zool Soc., Vol. 34, No. 9, p. 87.

All the specimens illustrated on this plate except that shown in Figures 4 and 6 are in the type collection of the Department of Paleontology of the California Academy of Sciences.

### PLATE II.

Fig. 1. *Aloidis (Caryocorbula) nuciformis* Sowerby. Hypotype, left valve, from Loc. 27570 (C.A.S.), dredged between the Gulf of Tehuantepec and Acapulco, Mexico; Templeton Crocker Exped., 1932. Length, 9.9 mm.; height, 8 mm. P. 241.

Fig. 2. *Rocellaria ovata* Sowerby. Hypotype, right valve, from Uvita Bay, Costa Rica. Length, 10 mm.; height, 4.8 mm. P. 246.

Fig. 3. *Aloidis (Caryocorbula) ventricosa* Adams & Reeve. Hypotype, right valve, from the same locality as the specimen shown in Fig. 1. Length, 12.2 mm.; height, 9.2 mm. P. 242.

Fig. 4. *Aloidis (Caryocorbula) ventricosa* Adams & Reeve. Hypotype, left valve, from the same locality as the specimen shown in Fig. 1. Length, 13.5 mm.; height, 9.4 mm. P. 242.

Fig. 5. *Sanguinolaria purpurca* Deshayes. Hypotype, left valve, from Station 135-D-25, San Lucas Bay, Lower California, Mexico, Lat. 22° 53′ N., Long. 109° 54′ W., dredged in 7 fathoms (13 meters). Length, 34 mm.; height, 20.9 mm. P. 219.

Fig. 6. *Jouannetia* (*Triomphalia*) *pectinata* Conrad. Hypotype, right valve, from Port Parker, Costa Rica. Length, 29 mm.; height, 21 mm. P. 248.

Fig. 7. *Tellina* (*Eurytellina*) *eburnea* Hanley. Hypotype, right valve, from Station 197-D-2, 7 miles west of Champerico, Guatemala, Lat. 14° 13′ N., Long. 92° 02′ W., dredged in 14 fathoms (25 meters). Length, 26.5 mm.; height, 17.5 mm.

This species was discussed in *Zoologica*, New York Zool. Soc., Vol. 34, No. 9, p. 73.

Fig. 8. *Sanguinolaria purpurea* Deshayes. Hypotype left valve. View of the interior of the specimen shown in Fig. 5.

Fig. 9. *Aloidis* (*Caryocorbula*) *nasuta* Sowerby. Hypotype, from Loc. 27584 (C.A.S.), about 10 miles due east of San Jose del Cabo, Lower California, Mexico, Lat. 23° 03′ to 23° 06′ N., Long. 109° 31′ to 109° 36′ W., dredged in 20-220 fathoms; Templeton Crocker Exped., 1932. Length, 12.1 mm.; height, 7 mm. View showing left valve and a portion of the right valve. P. 240.

Fig. 10. *Gari regularis* Carpenter. Hypotype, right valve, from Loc. 24074 (C.A.S.), off Ceralbo Island, Gulf of California (between Ceralbo Island and Arena Point, Lower California); F. Baker Coll. Length, 46.3 mm.; height, 25.0 mm. P. 218.

Fig. 11. *Aloidis* (*Caryocorbula*) *ovulata* Sowerby. Hypotype, left valve, from Loc. 27572 (C.A.S.), a few miles south of Acapulco, Mexico, dredged in 15-20 fathoms; Templeton Crocker Exped., 1932. Length, 23.6 mm.; height, 13 mm. P. 241.

Fig. 12. *Mactra* (*Mactrotoma*) *nasuta* Gould. Hypotype, left valve, from Loc. 24062 (C.A.S.), San Lucas Bay, Lower California, Mexico. Length, 66.5 mm.; height, 48.6 mm. P. 229.

Fig. 13. *Aloidis* (*Caryocorbula*) *porcella* Dall. Hypotype, right valve, from Station 126-D-12, east of Cedros Island, off the west coast of Lower California, Mexico, Lat. 28° 20′ N., Long. 115° 10′ 30″ W., dredged in 45 fathoms (82 meters). Length, 6.1 mm.; height, 4.3 mm. P. 242.

Fig. 14. *Mactra* (*Micromactra*) *angusta* Reeve. Hypotype, right valve, from Station 198-D-1, La Libertad, El Salvador, Lat. 13° 27′ 20″ N., Long. 89° 19′ 20″ W., dredged in 13 fathoms (24 meters). Length, 33.8 mm.; height, 21.6 mm. View of the interior.

Fig. 15. *Aloidis* (*Caryocorbula*) *porcella* Dall. Hypotype, right valve, from the same locality as the specimen shown in Fig. 13. Length, 7 mm.; height, 4.9 mm. View showing radial rows of pustules on posterior area. P. 242.

Fig. 16. *Mactra* (*Micromactra*) *fonsecana* Hertlein & Strong, sp. nov. Holotype, left valve, from Potosi and Monypenny Point, Nicaragua, in the Gulf of Fonseca. Length, 53.2 mm.; height, 34.5 mm. View of the interior. P. 232.

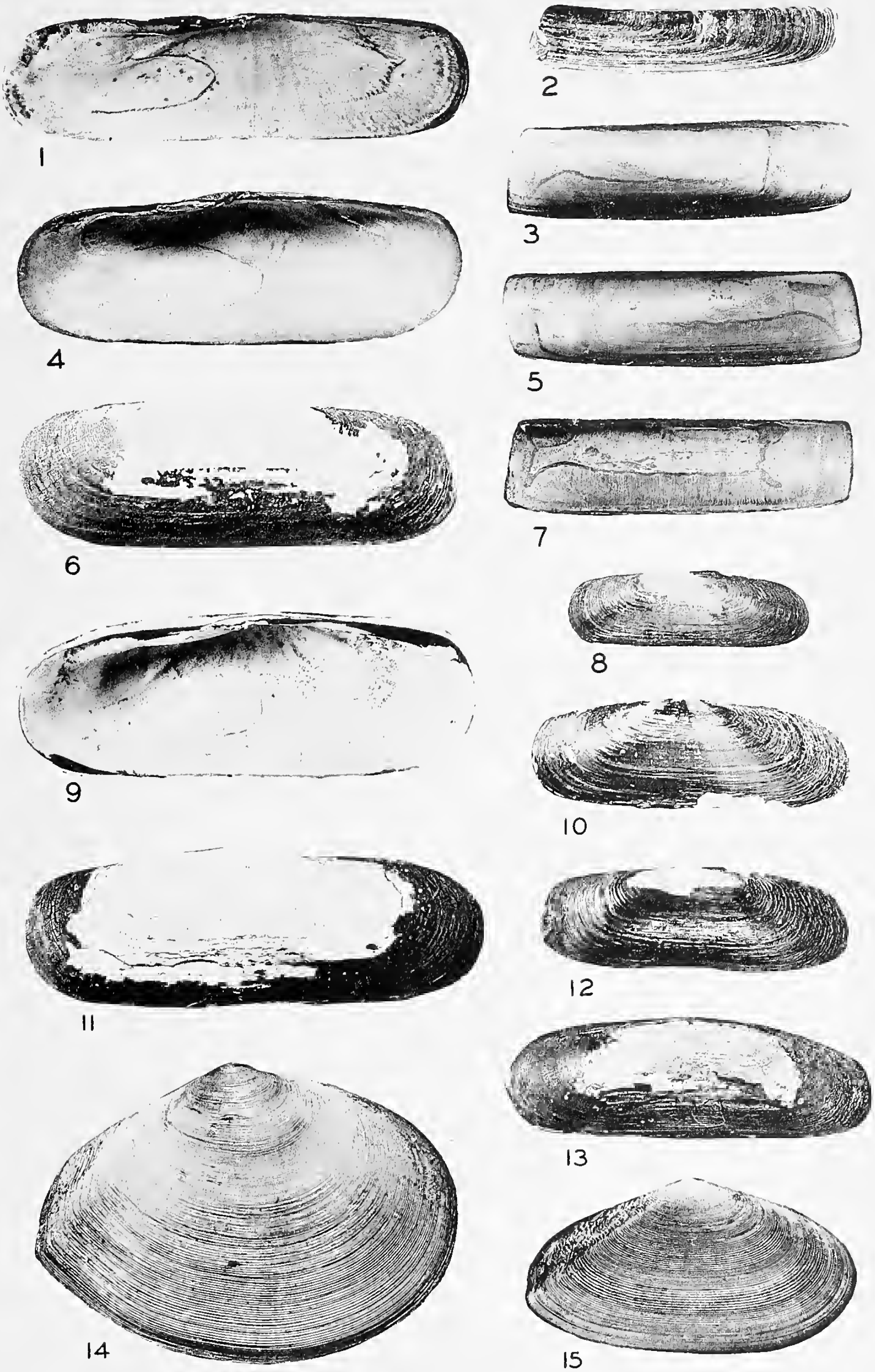
Fig. 17. *Aloidis* (*Caryocorbula*) *marmorata* Hinds. Hypotype, left valve, from Station 195-D-9, Port Guatulco, Mexico, Lat. 15° 44′ 28″ N., Long. 96° 07′ 51″ W., dredged in 7 fathoms (12.6 meters). Length, 7.0 mm.; height, 4.7 mm.

Fig. 18. *Mactra* (*Micromactra*) *angusta* Reeve. Hypotype, right valve. View of the exterior of the specimen shown in Fig. 14.

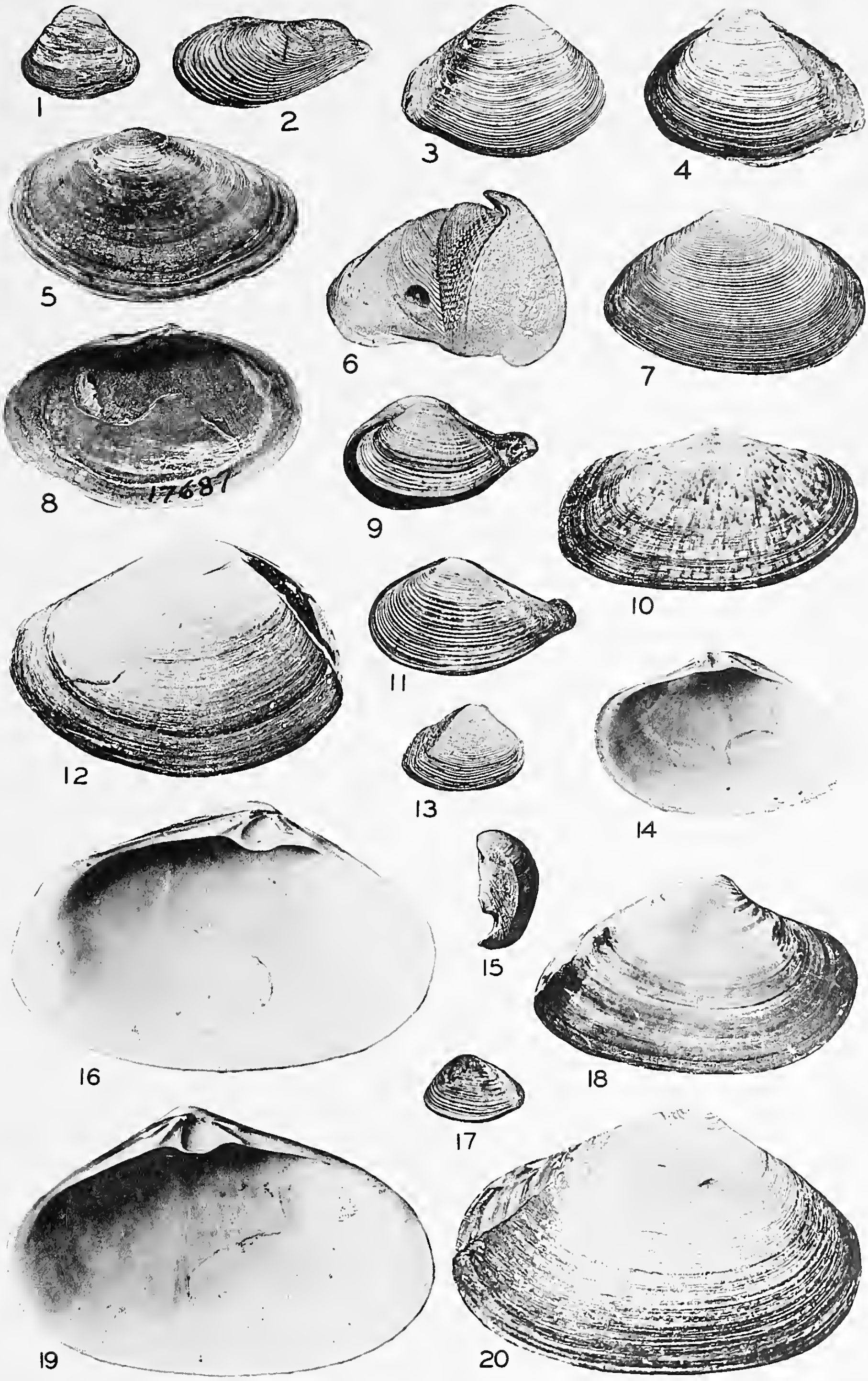
Fig. 19. *Mactra* (*Micromactra*) *fonsecana* Hertlein & Strong, sp. nov. Holotype. View of the interior of the right valve of the specimen shown in Fig. 16.

Fig. 20. *Mactra* (*Micromactra*) *fonsecana* Hertlein & Strong, sp. nov. Holotype. View of the exterior of the specimen shown in Fig. 19.

All the specimens illustrated on this plate are in the type collection of the Department of Paleontology of the California Academy of Sciences.




MOLLUSKS FROM THE WEST COAST OF MEXICO AND CENTRAL AMERICA. PART IX.




MOLLUSKS FROM THE WEST COAST OF MEXICO AND CENTRAL AMERICA. PART IX.

# 20.

# Comparative Biology of Salticid Spiders at Rancho Grande, Venezuela. Part V. Postembryological Development of Color and Pattern.[1]

JOCELYN CRANE.

*Research Zoologist, Department of Tropical Research, New York Zoological Society.*

[This is one of a series of papers resulting from the 45th, 46th and 47th Expeditions of the Department of Tropical Research of the New York Zoological Society, made during 1945, 1946 and 1948 under the direction of Dr. William Beebe, with headquarters at Rancho Grande in the National Park of Aragua, Venezuela. The expeditions were made possible through the generous cooperation of the National Government of Venezuela and of the Creole Petroleum Corporation.

[The characteristics of the research area are in brief as follows; Rancho Grande is located in north-central Venezuela (10° 21′ N. Lat., 67° 41′ W. Long.), 80 kilometers west of Caracas, at an elevation of 1,100 meters in the undisturbed montane rain forest which covers this part of the Caribbean range of the Andes. Adjacent ecological zones include seasonal forest, savanna, thorn woodland, cactus scrub, the fresh-water lake of Valencia and various marine littoral zones. The Rancho Grande area is generally subtropical, being uniformly cool and damp throughout the year because of the prevalence of the mountain cloud cap. The dry season extends from January into April. The average humidity during the expeditions, including parts of both wet and dry seasons, was 92.4%; the average temperature during the same period was 18° C.; the average annual rainfall over a five-year period was 174 cm. The flora is marked by an abundance of mosses, ferns and epiphytes of many kinds, as well as a few gigantic trees. For further details, see Beebe & Crane, *Zoologica*, Vol. 32, No. 5, 1947. Unless otherwise stated, the specimens discussed in the present paper were taken in the montane cloud forest zone, within a radius of one kilometer of Rancho Grande.]

## CONTENTS.



[1] Contribution No. 886, Department of Tropical Research, New York Zoological Society.

## INTRODUCTION.

This is the fifth of a series of papers dealing with the salticid spiders of Rancho Grande, Venezuela. Part I (Crane, 1948.1) discussed the taxonomy and life histories of three species of *Corythalia*, including postembryological development; Part II (1948.2) described methods of study; Part III (1949.1) dealt with systematics and behavior in the adults of eight new species and Part IV (1949.2) concerned display. The present paper is restricted to descriptions and comparisons of postembryological development of color and pattern in the same species considered in the previous sections.

Under each species, a résumé is given of the adult appearance; complete descriptions will be found under the type description or other quoted references. Descriptions of the young are given less fully than those of *Corythalia*, which were treated exhaustively in order to determine the range of variation in closely related species. In the present paper, the aim is rather to show general trends of pigment and pattern development in the various groups. To what extent they are metabolic, genetic, adaptive and vestigial remains largely in the realm of speculation; discussion of these theoretical considerations is being reserved until after publication of the remaining sections on postembryology.

Because of the range of intermediate steps between "hairs" and "scales," and their frequent occurrence in the young, the word "elements" will be used where a general term is needed to cover short, integumentary structures, sometimes called "protective" by earlier writers, and excluding bristles, trichobothria and spines. The standard abbreviations AME, ALE, PME and PLE are employed throughout for the various eyes, antero-median, antero-lateral, postero-median and postero-lateral, respectively. The terms "instar" and "stadium" are used interchangeably. The "first instar" corresponds to the "1. *Postembryonalstadium*" of Holm (1941).

Although many other immature individuals were collected, only those young have been included in the material for this paper in which colors were described in life, since fading in alcohol is even more prevalent in the young than in adults. Since few speci-

mens were reared throughout the life cycle, the correct instar names could be given only to the early ones, reared from the egg. Hence the terms "pre-pre-penultimate instar," "pre-penultimate instar" and "penultimate instar" are used, respectively, for the third stadium before the adult, the second before the adult and the preadult. These older juveniles were determined by rearing after capture in the half-grown state. Although middle instars, especially the fourth and fifth, are usually missing from the series, all of the species could undoubtedly be reared through the complete cycle, as in *Corythalia,* given sufficient time and care.

In the following descriptions, the black pigmentation of the eye capsules is not mentioned, since in every case this begins development late in the first instar, and is highly developed in the second. This is often supplemented externally by especially dense black pigment in the hypodermis of the eye tubercles, which is particularly conspicuous in those adult females and young having otherwise light-colored carapaces. Also unmentioned are the black tarsal pads and claws which are more or less pigmented from their appearance in the second instar; and the leg spines, which develop pigment gradually and sometimes become very dark by the middle instars, as in the plexippinids.

### Historical Review.

The vivid hues of salticid spiders have been remarked from the days of Wallace and before. As with birds and butterflies, however, the brilliance of a few has given a reputation to the entire group, a majority of which are not, to human eyes, conspicuous even in the adult. As in birds, bright pigments and structural iridescence are rarely found before the approach to maturity.

Very few studies have been made on the development of pigments and patterns in salticids. Wagner (1888, p. 296 ff.), who included salticids in his material, described the histology of tactile hairs during the molting of spiders; deposition of pigment, however, was barely mentioned. Later (pp. 361-362) he dealt with color development in very general terms, noting the frequent similarity of females and young, and the late development of adult male coloration.

The Peckhams occasionally mentioned color patterns of young salticids in connection with their discussions of secondary sexual characteristics and of species differences (1889, pp. 14-25, col. pl. I; 1909, p. 361, and in systematic section). They emphasized the similarity to pigmentation in birds, pointing out that when salticid males are more conspicuously colored than the females, the young usually resemble the females, and that when the adults are similar, the young resemble them both. The Peckhams were well aware of the gradual development of color, of the appearance of patterns at particular instars and of their probable phylogenetic significance; it is to be regretted that they published no papers devoted to the subject.

Moles (1916, p. 146) briefly described the color of young *Phidippus* sp., probably of the second instar, in California.

It remained for Bonnet (1933, pp. 132-133) to describe and figure the color patterns of the carapace and abdomen of a salticid, *Philaeus chrysops*, during all the instars. As with the Venezuelan species, the first instar after hatching (the *stade nymphal*) has a pale abdomen (yellow in this species). The second instar, also passed entirely within the cocoon, is metallic blackish-green all over; from the third instar (when the young leave the cocoon) through the penultimate, the sexes are both gray with black spots and bands, showing little change during growth and are roughly similar to the adult female. The black of the carapace increases, however, with succeeding molts, and in adults of both sexes the dorsal black abdominal bands develop into a median, longitudinal stripe. Only in the adult male does vermilion appear on the abdomen.

A few papers may be mentioned which are of particular importance in the study of salticid color development, although they concern it only indirectly:

Simon (1901) gave a résumé for each salticid subfamily of the general color characteristics in the various genera, while Di Caporiacco (1940) emphasized the importance of recording color variations in spider systematics because of their frequent genetic basis.

Apparently no work has been done from a biochemical point of view on the development of pigment in young salticids, although Millot's classic study of the histology of spiders in general gives an excellent basis for future work. He found (1926, p. 99) that the integumentary pigments are of four types, all excretory: guanin, responsible for white; melanin, for black, gray and dark brown; the caratinoids, which form yellow, orange and red; and a green pigment of undetermined affinities. Salticids are not mentioned specifically in his discussion of pigments, but he included three species of that family in his list of histiological material. Although he was speaking specifically of hypodermal and subhypodermal pigments of adults, visible through the translucent cuticle, the same excretory origin must hold for the superficial colored elements — hairs, scales and intermediate structures—which, along with the cuticle itself, also originate in the hypodermis, and are very prevalent in salticids of all ages.

As Millot points out, the hypodermal colors are not shed during ecdysis, and hence can be accumulated during life. Judging by their hues, these are principally melanins in salticids, with occasional deposits of guanin in the abdomen. It seems important, however, to emphasize a self-evident corollary which must apply in this family: since the colors of the elements are unchanged between molts (except perhaps through fading), and, indeed, are as superficial as are the scales of Lepidoptera, they are the result of chemical

processes which took place in the preceding instar from that in which they occur as external characteristics of the species. This is similar to the situation in many insects. For example, in pierid butterflies, pterine compounds, which are structurally similar to uric acid and generally regarded as excretory, are deposited in the wing scales during metamorphosis (Wigglesworth, 1939, p. 33 and ref.; Imms, 1948, p. 11 and ref.).

For the eventual understanding of arachnid coloration, we shall need to know the conditions necessary for pigment deposition. It has been found in insects that melanin is often laid down near areas of high metabolism, while guanin deposits are made in regions of low activity (Wigglesworth, 1939, pp. 333, 334). Hormones in insects and other invertebrates are known to be responsible for many color phenomena (Hanström, 1939, and ref.), just as in higher animals. Similar controlling factors unquestionably operate in these spiders.

## SYSTEMATIC ACCOUNT.

### LYSSOMANINAE.

**Lyssomanes bradyspilus** Crane (1949.1, p. 31).

*Adults and Young*: The three principal divisions of *Lyssomanes* pigmentation are the translucent green of the integument so characteristic of the genus, the black subintegumentary markings, and the white, yellow and orange-red superficial elements of the anterior carapace. Sexual dimorphism is slight.

In *L. bradyspilus*, from Rancho Grande, the green appears in pale form during the second instar, after emergence from the cocoon; in *L. beebei*, from British Guiana, it appears in the first instar according to Beebe (Crane, 1943, p. 126). The AME, however, acquire their first green a little later, at the end of the second instar. Immature *Lyssomanes* are often more yellowish than adults. In the latter, the green shows no regular sexual dimorphism, but individual variation in the tint is great.

Deep-lying black markings occur frequently in the genus, especially on the appendages, the dorsum and, more rarely, the carapace. In *bradyspilus*, they are highly variable, sometimes absent, never appear before the adult stadium, and develop only several days after the molt. The male has from one to four pairs of abdominal spots; females may have one or two pairs, in addition to some markings on the legs. The spots are fugitive in alcohol. In species from other localities, e.g. *nigropictus* Peckham, 1888, the spots are more numerous and relatively constant (Crane, *ibid*).

The colored elements of the anterior carapace develop during the middle instars, when the spider is about half grown and measures about 2 mm. in total length. At this time pale yellow patches appear on the inner (dorsal) sides of the dorsal eye tubercles, especially beside the ALE, while white hairs circle the AME and form a scanty clypeal band. The penultimate instars are similar except that both dorsal and clypeal scales are more plentiful; the dorsal groups may be mixed with white and show traces of orange-red on inner sides of the ALE tubercles. Adult females sometimes differ from penultimates in the addition of an orange-red crest behind AME; the adult male lacks this crest but has the white clypeal band replaced by orange-red.

In summary, the integumentary green of *Lyssomanes* develops in the earliest stages. Black subintegumentary markings are highly variable and appear, if at all, after the final molt; both sexes may have spots in the abdomen, females only in the legs. Colored elements appear in midgrowth, being yellow around the dorsal eyes and white on the clypeus; the sexes remain similar until the adult stage, when the clypeal band of the male is orange-red while the female may develop a crest of the same hue.

*Material*: First instar: 40 individuals (2 broods); second instar, 15 (same broods); middle instars, 5; penultimate males, 3; penultimate females, 3.

### MARPISSINAE.

**Menemerus bivittatus** (Dufour).

*Ref. to Color Descriptions: Attus mannii* Peckham, 1883, p. 27 (male only). *Menemerus melanognathus*, Peckham, 1888, p. 83 (male only). *Menemerus bivittatus*, Simon, 1901, p. 603; Petrunkevitch, 1925, p. 241. *Marpissa melanognatha*, Peckham, 1909, p. 483. *Marpissa bivittatus*, Comstock, 1940 ed., p. 686.

*Adults*: Color at Rancho Grande in both sexes characterized by white, gray, light rufous and brown elements which in various proportions cover the dark brown integument above; a strong, narrow, white submarginal band present on sides of carapace; large eyes rimmed with rufous scales; leg integument not deeply pigmented, well haired and scaled. Iridescence, the purer hues and strong blacks lacking. Sexual dimorphism moderate, best shown in the following regions: clypeus in male with a strong white band which in female is dull rufous (formed of light rufous and dull white elements). Subproximal chelicera band of white present in male only. Elements of carapace above much darker in male than female, except in central region; integument of appendages also darker in male, especially palp and first leg; other legs distinctly banded; although white appendage hairs are plentiful in both sexes, they are longer and more numerous in female, forming long fringes on anterior and posterior palp margins. Dorsum of male with a broad, median dark brown stripe flanked by grayish-white, the sides being brownish; female dorsum much lighter with a variegated pattern of white, gray and buff hairs, including some irregular and variable chevrons. Light hairs occur plentifully in both sexes on ventral surface. In brief, the male is distinguished by a white

rather than rufous clypeus, darker carapace and legs and a dark stripe on the dorsum, while the female has white-fringed palps and plentiful white elements on carapace and legs.

*First Instar*: Carapace and abdomen slate gray. Abdomen with basal median dark stripe and, in posterior half, a median light streak flanked by a pair of light blotches. Legs translucent and colorless.

*Second Instar*: Resemblance to adult female pronounced. Dorsal surface, including ocular quadrangle, median thoracic region and dorsum covered with close-set buffy-brown elements. The effect is formed of grayish-white and rufous elements. Abdomen with a pair of thin, weak, dark stripes, hardly visible, and some barely indicated chevrons. Integument dark brown. Sides of carapace and abdomen covered with rufous scales. Eyes all dark brown, rimmed with rufous scales, except dorsal part of AME which have whitish hairs. Clypeus and mouthparts scaleless, dark brown. Integument of all palps and legs translucent and colorless except for faint bands on joints from patella distally. Palps plentifully clothed with white hair, but without the pronounced marginal fringes of adult female; legs similarly clothed to a lesser extent, their hairs quite short. Sternum black; venter translucent grayish with very sparse, light hairs.

This second instar differs from adult females as follows: white submarginal carapace band absent; sides of carapace and abdomen more rufous, not dark brown; dorsal elements paler and more homogeneous; clypeus naked, although a few rufous hairs are present on cheeks; palps and legs mostly unpigmented; sternum and venter hairier.

*Pre-pre-penultimate Instar, Male*: (Probably *Fifth Instar*): Carapace length 2.02 mm. By this stadium the clypeus has rufous elements well developed, but still lacks white. Submarginal white carapace band fully developed. There are no other changes of note.

*Pre-penultimate Instar, Male*: No change from preceding.

*Penultimate Instar, Male*: Differs noticeably from adult female only in lack of white palpal fringes and in relatively few white leg hairs.

*Penultimate Instar, Female*: White palpal fringes and hairs on legs still underdeveloped.

*In summary*, there is a close resemblance to the adult female even in the second instar; the white submarginal carapace band and rufous clypeal hairs probably appear in the third or fourth instar; white clypeal hairs do not mingle with the rufous until the penultimate male instar. The characteristic pure white clypeal band, dark legs and dark abdominal stripe of the male, and the white palpal fringes of the female, appear only in the final instar.

Comparison with published color descriptions indicate that Florida specimens are more rufous than adult tropical forms; young Rancho Grande specimens show more rufous elements than the browner and grayer adults. These general scale and hair colorings and a white submarginal carapace band are characteristic of the genus (Simon, 1901, p. 603).

*Material*: 1st instar: 10 (2 broods); 2nd instar: 14 (1 brood); pre-pre-penultimate instar, male, 3; pre-penultimate instar, male, 3; penultimate instar, male, 3, female, 4.

## Synagelinae.

**Semorina brachychelyne** Crane (1949.1, p. 35).

*Adults*: General color brown, scaleless, nearly hairless except for fine hairs on abdomen and a few on appendages; the elongated first legs are darker than the very pale remainder in both sexes. Eyes brown, shifting to black, rimmed scantily with yellow hairs. Sexual dimorphism moderate: in male, palps and first legs much darker than in female; two spots of flat-lying silvery-white hairs on abdomen. In female, general color paler brown, slightly yellowish; tibia and tarsus of palps dorsally with silvery-white hairs; abdominal markings a dark stripe with several dark cross-bars.

*First Instar*: Pigment lacking.

*Penultimate Instar, Male*: Paler than adult; first legs scarcely darker than remainder, except for anterior (inner) surface of femur which has pigment strongly developed; white abdominal spots present, but inconspicuous.

*Material*: First instar, 3 (1 brood); penultimate males, 2.

## Dendryphantinae.

**Ashtabula furcillata** Crane (1949.1, p. 39).

*Adults*: Carapace and abdomen above covered with iridescent green scales; a white stripe around sides of carapace and around abdomen; AME rimmed with yellowish scales; first legs dark, remainder pale.

Sexual dimorphism slight: male palps black, female pale greenish-yellow; first legs and sides of carapace black in male, brown in female.

*Penultimate Instar, Male*: Similar to adult male, but palps greenish-yellow and first legs brown, as in female. Dorsal scales iridescent greenish-bronze, that is, less green than in adult. Abdomen laterally with a dark brown stripe below the usual white stripe of the adult; below this is an iridescent greenish stripe extending partly on venter, as in adult. Sternum and venter brown.

*Penultimate Instar, Female*: Entire upper surface, carapace and abdomen, covered closely with bluish-gray, non-iridescent scales, bounded laterally from ALE to spinnerets by the usual white stripe of the adult. Clypeus and sides of carapace naked brown. Carapace with a narrow submarginal white border of scales. AME chestnut. Eyes all rimmed completely with white, not yellow. Chelicerae and sternum light brown. Palps pale lemon yellow. Legs entirely translucent

horn, the first legs darker brown like sides of carapace, the first femur anteriorly almost black. A white spot above spinnerets at base. Underside of abdomen almost black with some gray hairs laterally.

*Material*: Penultimate instar, male, 2, female, 1.

**Sassacus flavicinctus** Crane (1949.1, p. 41).

*Adult Male*: Integument black with lemon yellow elements as follows: on carapace, in a pair of dorso-lateral, converging stripes below eyes, a submarginal band and a clypeal band and, on abdomen, a subbasal band, two pairs of dorso-lateral bands and, sometimes, a subdistal spot. Abdomen otherwise covered with black elements. Front eyes rimmed with rufous elements. Integument of legs black in proximal segments, paler and banded distally, the first leg darker; variable yellow and white hairs and scales on proximal segments anteriorly. Sternum and venter with white hairs.

*Adult Female*: Sexual dimorphism extreme. General color brown with obscure markings of ochraceous, not lemon yellow: Carapace integument black covered with close-set, monotone, ochraceous brown elements absent only in middle of ocular quadrangle; palps dark with dull yellow hairs; integument of legs banded; dorsum covered with ochraceous brown elements with a reticulated pattern of lighter ochraceous, including a subbasal band.

*First Instar*: Carapace gray, darkening with age. Coxa, trochanter and femur of all legs dark gray, other segments translucent and colorless; abdomen pale greenish-yellow to grayish-green.

*Second Instar*: Integument of carapace and abdomen black, completely covered above with a moderately close sprinkling of grayish or greenish-white short hairs. Large eyes rimmed with similar hairs. Integument of legs all conspicuously banded light and dark.

*Pre-penultimate Instar, Male*: Like adult male, the lemon yellow markings being well developed except that those on carapace are paler and narrower; second pair of abdominal bands may meet in midline; no subdistal abdominal spot; dark scales in middle of dorsum brown, not black; patches of light hairs on legs at distal tips of second, third and fourth femora only. Hairs on underside scanty but in typical arrangement.

*Penultimate Instar, Male*: Lemon yellow carapace markings now of adult width and intensity, but legs and abdomen as in preceding stage.

*Penultimate Instar, Female*: Differs from adult in presence of a definite carapace band of ochraceous or light brown scales among the dark brown elements, passing below ocular quadrangle and behind it across thorax. Abdominal reticulations more obscure than in adult.

*Material*: 1st instar, 15 (2 broods); 2nd, 10 (2 broods); pre-penultimate male, 1; penultimate male, 3; penultimate female, 2.

**Sassacus ocellatus** Crane (1949.1, p. 34).

*Adults*: In both sexes, integument of carapace and abdomen black covered above with iridescent green scales, with a pair of black spots, each crossed by a white bar, near tip of abdomen; clypeus white; second, third and fourth legs brown.

Sexual dimorphism slight: a submarginal white carapace band present in female only, and her face with more white elements; integument of palps and first legs black in male; palps banded in female, and first legs brown, except for black femur; white scales on distal segments of legs in male only; a subbasal pale abdominal band in female only.

*First Instar*: Carapace dark gray; abdomen pale green; legs translucent and colorless.

*Penultimate Instar, Male and Female*: Differs from adult as follows: iridescence less well developed, bronze green rather than emerald; palps pale except for darker femur; first legs paler than adult and all other legs well banded at joints, not uniform brown; a few yellowish-white scales on first leg only, anteriorly only; a narrow white submarginal carapace band as in female; a subbasal abdominal band extending well along sides, also as in female; above this, in the black, non-iridescent stripe, are three pairs of white, dorso-lateral cross-bars, the first two very faint, the most posterior strong and persisting in the adult.

*Material*: First instar 6 (1 brood); penultimate instar, males 4, female 1.

## Hyllinae.

**Phiale** spp.

The *Phiale* of the Rancho Grande region include at least three species, of which one, from Rancho Grande itself, has been described as new (*P. flammea* Crane, 1949.1, p. 47). *P. dybowskii* (Taczanowski, 1871) occurs at somewhat lower altitudes; in color it checks perfectly with Chickering's description (1948, p. 217). A third species is highly variable and remains undescribed for lack of an adequate series; it is fairly common and overlaps the ranges of both *flammea* and *dybowskii*. Young of most stadia of presumably all three forms are taken plentifully in June, July and August, but because of their great individual variation, the presence of the poorly defined third species and the essential similarity of the young, it was found impossible to identify the latter without rearing them to the adult. Time limitations prevented this except for several pre-penultimate instars in each species, the first two instars of *flammea* and the first four of *dybowskii*. The male probably passes through seven to eight stadia, depending on the species. The young are relatively easy to rear, and would form an excellent subject for intra-generic comparison studies. Since the course of color development is so similar, it will be sketched below in general terms; the crucial specific differences generally emerge only in the final instar.

*Adults*: Carapace integument black with a submarginal band of white or creamy scales extending from near pedicel completely around clypeus; above with more or less black or rusty scales and with a median white stripe and/or spots. Abdomen covered with scales ranging from rusty black to brilliant flame scarlet with a subbasal white band extending halfway along sides; a white cross-bar present at least underneath scales; one or more white distal spots usually apparent.

Sexual dimorphism moderate. White or cream carapace bands all more extensive in male than in female, while the remainder of the carapace scales tend to be black, not brown or rusty. Anterior eyes rimmed with rufous in male, with paler in female; palps and at least first legs spotted with white elements in male, paler with few or no white elements in female. Scales of abdomen redder in male than in female, in which it is often more brown than rufous and sometimes practically black; white abdominal markings tend to be overlaid in the male by the rufous scales, particularly in *flammea*. Distal white spots always larger and more conspicuous in female.

*First Instar* (*P. dybowskii and P. flammea*): Carapace gray; abdomen greenish-yellow to olive green; appendages translucent and colorless.

*Second Instar* (*P. dybowskii and P. flammea*): Carapace and abdomen jet black, scaleless, short black hairs scattered on ocular quadrangle and abdomen. AME and ALE surrounded completely by a scanty fringe of relatively long hairs, white around lower AME and all ALE, light rusty around upper half of AME. All eyes jet black. Chelicerae black. Black pigment present at least proximally at least in palp and first leg in both species; banding may occur in third and fourth legs in *flammea*, markings longitudinal in *dybowskii*.

*Third Instar* (*P. dybowskii*): Differs from second in presence of two pairs of short, lateral, white abdominal bars, one toward middle of length and one behind; a few rusty hairs across middle of abdomen; a faint median pale abdominal spot; ocular quadrangle with a scanty covering of dull brown scales.

*Fourth Instar* (*P. dybowskii*): Differs from third in bronze sheen of ocular qualrangle scales, in presence of a short, slender, subbasal white abdominal band; two pairs of lateral white bars of the third instar are now only spots; median spot now extended as a broad, faint cross-bar, the central spot remaining strong. No white on clypeus; rust around anterior eyes present; slightly more black pigment on legs.

*Pre-penultimate Instar, Males and Females, All Species*: Carapace scalation now about as well developed as in adult females, including white band and clypeal hairs. Legs still with less black pigment than in adult and few or no white scales. Abdomen black, only tinged with rufous, the white bands strongly edged with black.

*Penultimate Instar, Males and Females, All Species*: Similar to adult females, but fine specific color distinctions, such as the terminal hooks on the subbasal abdominal band of *dybowskii*, are not yet developed. White palp and leg scales less numerous than in adult females.

*Material*: *P. dybowskii*: first instar, 10; second, 10; third, 4; fourth, 3; all first four instars from a single brood; pre-penultimate instar, male, 1, female, 1; penultimate instar, male, 3, female, 2. *P. flammea*: first instar, 15 (3 broods); second instar, 10 (4 broods); pre-penultimate instar, males, 2, females, 3; penultimate instar, males, 4, females, 4. *Phiale* spp.: Pre-penultimate and penultimate instars, males and females, records made of pattern variations only, 19 (not all reared to adult).

## Plexippinae.

### **Corythalia** spp.

The development of color and pattern in three species of Rancho Grande *Corythalia* has already been traced in detail (Crane, 1948, pp. 15-17, 24-25, 29-33; general résumé on pp. 3 ff. and Text-fig. 2.

The following *errata* should be noted in that publication: In the figures and descriptions of the stadia of C. *xanthopa* it was assumed that there were 7 male and 8 female instars, as in *C. chalcea* and *fulgipedia*, although *xanthopa* had not been reared throughout its cycle. During a subsequent season at Rancho Grande, examples of both sexes completed development from egg to adult. There proved to be only 6 male and 7 female instars. (This might have been expected from the smaller size of the adult, although there was an unusually large size increase after the third instar in the earlier material; see *ibid*, Text-fig. 11). Therefore, no instar was missing after all from the published series, and the following corrections should be made concerning the *xanthopa* color descriptions: Text-fig. 2 (opp. p. 4): T - X, incl., actually represent the 4th, 5th male, 6th female, 7th female (adult) and 6th male (adult), respectively. The correspondence of the instar positions in the three species is, however, unchanged, since the prepenultimate, penultimate and adult stadia in each species are still comparable, regardless of the number of the instar. Similar shifts, to one instar number lower, should be made in the text on pp. 30, 32 and 33, namely: "Fourth Instar: Unknown" should be eliminated; for "fifth instar" read "fourth," for "sixth" read "fifth" and for "seventh" read "sixth" throughout.

## Magoninae.

### **Mago dentichelis** Crane (1949.1, p. 49).

*Adults*: In both sexes, carapace integument black with a median stripe of white scales enclosing a central black spot. Sparse chestnut and black hairs around and near

eyes. Abdomen covered with brown, mixed with gray and white, scales in a variable, somewhat lyre-shaped, whitish marking, including a subbasal band; a pair of subdistal spots.

Sexual dimorphism slight. Palps black in male, pale in female; first two legs except tarsi black in male, other legs banded, whereas all legs are banded in female; white elements present on appendages in male, scanty or absent in female; posterior abdominal spots more distinct and constant in male.

*First Instar*: Carapace and legs translucent white; abdomen pale translucent yellow with three pairs of irregular, dark gray, dorsal blotches and a fourth pair, at extreme base, running laterally. The most distal pair join across the abdomen as a bar.

*Second Instar*: Carapace, abdomen and legs all pale translucent buff with strong black markings. Ocular quadrangle with a thin frosting of coarse yellow hairs, especially around all eyes including front. Immediately behind each posterior eye is a curved spot and a pair of curved bars on either side of midline at same level. Midway down thoracic slope a pair of shorter curved bars and on mid-side of carapace, just behind eye level, a long horizontal bar; carapace is bordered narrowly with black from level of first leg to just before pedicel. Face and chelicerae naked and translucent (except around eyes) as are palps except for black tip of femur and all patella. Sternum translucent. All legs strongly banded with black at joints except coxae and trochanters, the latter having a single spot.

Abdomen with a pair of basal dark spots, then a narrow cross-bar, interrupted in middle, followed by a midline group of irregular spots, though posteriorly there are two larger ones; this group is just behind high point of abdomen. Behind this is a pair of L-shaped markings, then a narrow cross-bar, convex anteriorly, the median part preceded by a still narrower, almost contiguous bar. Finally a pair of terminal black spots, touching spinnerets. Some long hairs all over abdomen and legs. Venter with some white, flat-lying hairs.

*Penultimate Instar, Male*: Differs from adult in relative inconspicuousness of the abdominal lyre-shaped pattern. The dominant markings, instead, are three pairs of small pale buff spots, in posterior half of abdomen.

*Material*: First instar, 13 (2 broods); second, 7 (1 brood); penultimate male, 1.

## Summary and Conclusions.

A brief general survey of salticid color development will now be made, based on the juvenile and adult material of the eleven species specially treated in this and preceding papers of the series. These species were selected as characteristic of their respective subfamilies and are widely distributed systematically throughout the family; they illustrate the principal characteristics of salticid coloration and sexual dimorphism.

The regions of the body will be considered in turn. As usual, a distinction will be maintained between the colors of the integument and that of the colored elements, the hairs and scales, which overlie them. Often these elements are in sharp contrast to the generally dark integument, and the distinction is valid. Sometimes, however, the two structures bear a close color relation to each other. For example, female palps may have both pale integument and long white fringes, as in *Menemerus* and *Semorina*. Again, generically constant pale abdominal bands appear hypodermally in *Corythalia* in the scaleless first instar, and are later covered by corresponding bands of light-colored scales.

*Integument*: Carapace and abdomen nearly or quite colorless on hatching, but hypodermal pigment, visible as dull gray or green, develops toward the end of the stadium. When the spider is very black in adults of both sexes, the carapace is completely black in the second instar; this is true in *Sassacus* (Dendryphantinae), *Phiale* (Hyllinae) and *Corythalia* (Plexippinae). In others, where the adult is brown, or black only in the male, it darkens gradually, as in *Mago dentichelis* and an undescribed species of *Hypaeus* (both Magoninae).

The appendages develop pigment more slowly, even those that are completely black in the adult. They are sometimes quite colorless up to the middle instars; usually they are pigmented proximally or lightly banded at the joints, as early as the second.

Special patches of iridescent integument, as on the chelicerae of some dendryphantinids or the legs of *Corythalia*, appear only in the adult male.

*Hairs, Scales and Intermediate Elements*: These are conveniently divided into eleven rather well defined areas which appear throughout the salticids, regardless of subfamily.

1. Circumorbital markings: Along with the hairs of the dorsum, these are the most universally present and earliest-appearing of the colored elements. They appear around the AME and sometimes other eyes in the second instar, in all species studied except *Lyssomanes;* in the latter they develop later. When they first appear they are white, light yellow or rufous; in adults they range from orange to rufous. They are little variable intraspecifically, although they are sometimes brighter in males, as in *Phiale*.

2. Postorbital crest: Rare; white to orange-red; appears in adult only, male or female. When present, of variable length and thickness. Examples: *Lyssomanes bradyspilus; Hypaeus* sp. (undescribed).

3. Dorsal carapace: Including ocular quadrangle, region immediately below it, and thoracic region. Very variable within every species in adults, the female usually hairier or scalier than the male; in fact, these regions are sometimes more nearly naked in the adult male than in the penultimate. The elements may appear as a dense covering in

the second instar or, more usually, not before the third. Although all colors may be present, white stripes or spots are most frequent among striking dorsal markings at all ages (Examples: *Phiale; Corythalia fulgipedia; Mago dentichelis*). Sometimes (*Sassacus flavicinctus*) paired stripes appear as a secondary sexual character in the male, although they are indicated in the penultimate female.

4. Submarginal carapace band: Very common, as in many other families. White, cream or yellow; wide or narrow; sexual dimorphism various; better developed in adult male *Phiale* than in female, but secondarily lost in adult male *Sassacus ocellatus;* or dimorphism may be negligible as in *Corythalia fulgipedia.* May show considerable individual variation or practically none. Appears in third instar or later.

5. Clypeal band: Extremely common. Any color or mixture, but most common form is a strong white band which is strongly developed only in adult male (example: *Menemerus bivittatus*). Female may have an equal number of elements, but they are rarely of a single color and their disposition is not so exact; they often extend up over the cheeks. Elements sometimes secondarily reduced in adult male, giving a practically naked black clypeus, as in *Corythalia chalcea* and *fulgipedia.* Little intraspecific variation. First hairs appear in middle instars.

6. Chelicerae and mouthparts: Usually nearly naked throughout development except for marginal brushes and a few unspecialized hairs; adult male sometimes with a proximal anterior brush of long hair on chelicerae supplementing the clypeal band.

7. Palps: Often show considerable sexual dimorphism in adults. In the female may be pale and fringed with long white hairs (*Menemerus bivittatus, Semorina*), while the corresponding male palps are dark and lack fringes. In others, the female palps are medium brown while the males are black with anterior patches of shiny white or yellow scales (*Phiale*; *Corythalia xanthopa*). These extreme examples of sexual dimorphism appear only in the adult. Palps of the young always have some hairs, even in the first instar; later, both dark and light elements are present.

8. Legs: When the first legs of adult males are darker than the others, they are sometimes furnished anteriorly with bands or spots of white scales, as in *Phiale.* Usually they are also present, though fewer, posteriorly and on the other legs. These white scales may be mixed with scales of other colors in females and young, where they may be much more numerous, but not in the contrasting pattern of the male. The female too may have fewer pale leg scales than during earlier instars, as in *Corythalia fulgipedia.* In some species striking fringes appear abruptly in adult males, on legs active in display (*Corythalia* spp.). General hairiness, highly variable individually, is a usual growth character, appearing even in the first instar; the hairs usually become darker with succeeding stadia.

9. Sternum: Usually not very hairy, and the hairs are unspecialized, being short but not scaly, ranging from pale to black, and increasing in number from the earliest instars.

10. Dorsum: A few long hairs present in first instar; bands or spots or a general covering characteristic of the genus sometimes present in the second, formed of a few relatively large scales (*Corythalia; Sassacus*). By the middle instars, if not before, the dorsum is completely covered with elements ranging from hairs to full scales. Various chevron-like patterns, which prevail so widely in spiders, may be present, particularly in the young (as in *Menemerus bivittatus*). Details of the dorsal pattern are often highly variable after the middle instars. Iridescence appears in mid-growth in species of which it is a characteristic, and develops gradually; sometimes, as in *Ashtabula furcillata,* the iridescent covering of the dorsum may be continuous with that of the upper part of the carapace. In the same species is illustrated the occasional continuation of the submarginal carapace band down the length of the abdomen. A pale subbasal abdominal band is found widely throughout the family, at least in females (examples: *Sassacus, Phiale, Corythalia, Mago dentichelis*); in *Corythalia* it appears in the second instar; in the other forms it develops later.

11. Venter: Usually hairier than sternum; a drab pattern, often involving longitudinal stripes, is usually present from an early instar.

* * *

In brief, the first pigments to develop are the hypodermal melanins of eyes, carapace and abdomen, along with variously colored hairs and scales, chiefly circumorbital and abdominal. The white submarginal carapace band, if any, appears fairly early, as does the subbasal abdominal band. The hypodermal melanin of the appendages is deposited gradually throughout the instars, and is usually most intense in the chelicerae, palps and first legs of adult males. White hairs and scales on carapace and legs sometimes are most numerous in both sexes in the penultimate instar, being secondarily reduced at least in the adult male. Iridescent scales develop gradually in the middle instars, but reach maximum development only in the adult, usually in the male. Last to appear are many sexually dimorphic specializations, such as shiny white clypeal bands and palpal patches of specialized scales and scale hairs, cephalic crests, appendage fringes, areas of intense yellow, orange or scarlet scales, and secondarily naked patches of iridescent cuticle.

Because of the late appearance of these specializations, sexual dimorphism of pattern and color is usually not apparent before the penultimate instar of the male and often not until after the final male molt.

It is obvious, as pointed out years ago by the Peckhams, that this general course of color development parallels that of many animal groups, for example birds and fishes, in addition to that of spiders as a whole. There is the usual gradual increase in pigment, the young frequently resemble the adult female and there is often a striking change in the adult male consisting of the appearance of more intense and more contrasting pigmentary or structural colors.

Of special interest in this comparative study of a family are the clues to phylogenetic relationships, to be considered in a subsequent paper. As stated above, the order of development of the various components and areas of color are similar, regardless of the phylogenetic position of the genus or subfamily. It seems apparent, however, that juvenile pigment patterns, as well as the time of their appearance and the variability of the pattern elements, furnish some hints of species relationships within a genus, which are useful when used in connection with other evidence. At present they are of little help in tracing affinities in higher categories. When up-to-date studies, both chemical and genetic, can be made of the pigments at various instars in the various species, the usefulness of pattern and color in tracing phylogeny will doubtless be extended.

## References.


Beebe, W., & Crane, J.

1947. Ecology of Rancho Grande, a subtropical cloud forest in northern Venezuela. *Zoologica*, Vol. 32, No. 5, pp. 43-60.

Bonnet, P.

1933. Cycle vital de *Philaeus chrysops* Poda. *Arch. Zool. Expér.*, Vol. 75, pp. 129-700.

Caporiacco, L. Di

1940. Il valore delle variazioni di colorazione negli Aracnidi. *Redia*, Vol. 26, pp. 221-237.

Chickering, A. M.

1946. The Salticidae (Spiders) of Panama. *Bull. Mus. Comp. Zool., Harvard Coll.*, Vol. 97.

Comstock, J. H.

1940. The spider book. Doubleday, Doran & Co., N. Y. 1940 ed. revised & ed. by W. J. Gertsch.

Crane, J.

1943. Spiders of the families Lyssomanidae and Salticidae (Magoninae) from British Guiana and Venezuela. *Zoologica*, Vol. 28, pp. 125-138.

1948.1. Comparative biology of salticid spiders at Rancho Grande, Venezuela. Part I. Systematics and life histories in *Corythalia*. *Zoologica*, Vol. 33, pp. 1-38.

1948.2. Comparative biology of salticid spiders at Rancho Grande, Venezuela. Part II. Methods of collection, culture, observation and experiment. *Zoologica*, Vol. 33, pp. 139-145.

1949.1. Comparative biology of salticid spiders at Rancho Grande, Venezuela. Part III. Systematics and behavior in representative new species. *Zoologica*, Vol. 34, pp. 31-52.

1949.2. Comparative biology of salticid spiders at Rancho Grande, Venezuela. Part IV. An analysis of display. *Zoologica*, Vol. 34, pp. 159-214.

Hånstrom, B.

1939. Hormones in invertebrates. Oxford University Press, New York. ix + 198 pp.

Holm, A.

1941. Studien über die Entwicklung und Entwicklungsbiologie der Spinnen. *Zoologiska bidrag från Uppsala*, Vol. 19, pp. 1-214.

Imms, A. D.

1948. A general textbook of entomology. Seventh edition. E. P. Dutton & Co., New York.

Millot, J.

1926. Contribution a l'histophysiologie des Araneides. *Bull. Biol. France et Belgique*, Suppl. 8, pp. 1-238.

Moles, M. L.

1916. Growth and color patterns in spiders. *Jour. Entom. & Zool. Pomona Coll.*, Claremont, California, Vol. 8, pp. 129-150.

Peckham, G. W. and E. G.

1888. Attidae of North America. *Trans. Wisc. Acad. Sci. Arts Let.*, Vol. 7, pp. 1-104.

1889. Observations on sexual selection in spiders of the family Attidae. *Occ. Papers Nat. Hist. Soc. Wisconsin*, Vol. 1, pp. 3-60.

1909. Revision of the Attidae of North America. *Trans. Wisc. Acad. Sci. Arts Let.*, Vol. 16, pp. 355-646.

Petrunkevitch, A.

1925. Arachnida from Panama. *Trans. Conn. Acad. Arts & Sci.*, Vol. 27, pp. 51-248.

Simon, E.

1901. Histoire naturelle des Araignées. Vol. II, pp. 381-429.

Taczanowski, L.

1871. Les Araneides de la Guyane francaise. *Horae Soc. Entom. Ross.*, Vol. 8, pp. 32-132.

Wagner, W.

1888. La mue des Araignées. *Ann. Sci. Nat.*, Ser. 7 (*Zoologie*), Vol. 6, pp. 280-293.

Wigglesworth, V. B.

1939. The principles of insect physiology. E. P. Dutton & Co., London, New York. 434 pp.

# INDEX

Names in **bold face** indicate new genera, species or varieties; numbers in **bold face** indicate illustrations; numbers in parentheses are the series numbers of papers containing the plates listed immediately following.